





MADROÑO
A WEST AMERICAN JOURNAL OF BOTANY
VOLUME XXXIV
1987

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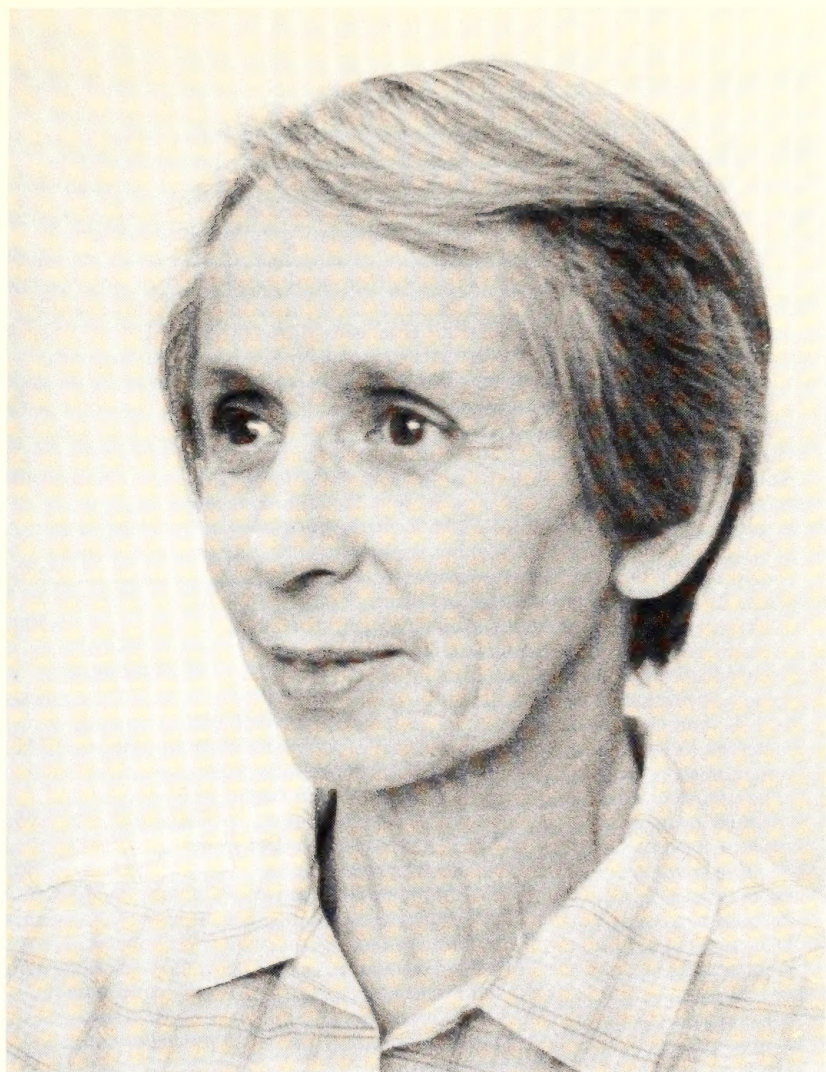
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Few botanists have had a more profound impact on the fields of plant reproductive biology and evolutionary ecology than Herbert and Irene Baker. For almost half a century, they have pioneered the study of plant reproductive systems, with major contributions ranging from Herbert's classical early work on the evolutionary importance of variation in plant breeding systems to Herbert and Irene's definitive recent work on the ecological significance of pollen, nectar, and fruit chemistry. In addition, Herbert has contributed many seminal ideas toward understanding the evolutionary ecology of colonizing species and weedy species. Yet, in many ways, the most



enduring impact that Herbert and Irene have had is on the many students, colleagues, and friends who have taken their legendary ecology courses at the University of California, accompanied them on field trips in California, Costa Rica, and elsewhere, or attended the stimulating and pun-filled evening meetings at their home in the Berkeley hills. Their contagious enthusiasm, quick wit, and unlimited interest in sharing insights about plant ecology and evolutionary biology have served as a continual source of inspiration. In return, it is with fondest affection that we dedicate this volume of *Madroño* to them.

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The Executive Council of the California Botanical Society has initiated a new policy for page charges. Starting with papers received by the editor after 31 Dec 1987, each author will receive five free pages per volume of *Madroño*. The decrease from 20 free pages every two volumes is necessary because of the escalating costs of publication. We wish to maintain the size and quality of issues, and this will be possible only with greater financial commitment from authors. We greatly appreciate the many papers contributed to *Madroño* and look forward to serving the membership and botanical community with quality volumes in the future.

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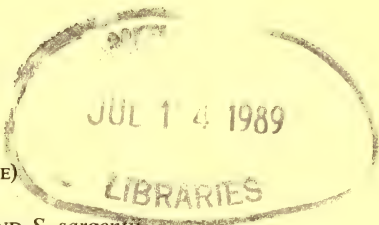
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MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

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ROOTS OF THE CALIFORNIA BOTANICAL SOCIETY*

JOSEPH EWAN†

Department of Biology, Tulane University,
New Orleans, LA 70118

ABSTRACT

The historic roots of the California Botanical Society are traced from 1853, when the California Academy of Natural Sciences was founded, to the organizational meeting in 1913 called by W. L. Jepson. Twenty-five organizations and events more or less influenced the Society's origins. Natural history events, especially botanical, in the East, the role of the California Botanical Club, the Sierra Club, and rivalries are noted particularly.

"Some time there will be here in Berkeley a wild-flower protection society, just as in the older states Some time, gentle reader, the call will come down from the mountain top . . . and everywhere the expression of the overmastering desire—the love of life." This from a short essay published by Jepson in 1898 entitled "The Love of Life".¹

The historian of the sciences must divest prejudices and special interests of his own age, so far as that is possible, and migrate into a strange land to bring back as unbiased an account as he can of what he has learned. He must not treat the past as one in spirit with the present. To paraphrase William Ferguson,² we must be alive to the existence of many different pasts, leading without predetermined succession, much less a progression. The historian pursues the facts and fastens upon them. "The dead were and are not. Their place knows them no more and is ours today. Yet they were once as real as we and we shall tomorrow be shadows like them."³ Perhaps we should remember Montesquieu: in the infancy of societies, the chief shapes the institution; later the society shapes the chief.

Were there differences between the Eastern and Californian devotees of botany? Botanists beach-combed Boston harbor for European ballast weeds and excitedly published their trophies in the *Bulletin* of the Torrey Club or *Rhodora*. Californians found stowaways from Chile or Mazatlan. Sometimes they asked "is it native?" or "are birds carrying the seeds?" Compared with the flora of the Eastern United States, California proved rich in endemics. Indian uses of plants had been studied, too. In the Mother Lode it was Digger Indians amid the Digger pines. Jepson called anthropologist Pliny Earle Goddard "my traveling companion on an expedition to

* Presented in shorter form at the Annual Banquet of the Society at Berkeley on 22 February 1986. † Present address: Missouri Botanical Garden, St. Louis, MO 63166-0299.

the South Fork of the Salmon River in 1902", where Goddard was noting the food and ceremonial plants of the Hupa tribe.

ALBERT KELLOGG AND THE ACADEMY

Roots of the California Botanical Society (CBS) may be traced back to the pioneering spirit of Albert Kellogg, who with three other doctors, a real estate agent, and a school superintendent met to organize the California Academy of Natural Sciences (Fig. 1). From Kellogg's taste, botanical discoveries dominated the Academy's deliberations. During the first decade 123 papers were published of which 43 concerned trees and flowering plants.

When Dr. Kellogg arrived in Sacramento on 8 August 1849, he surely brought the argonaut spirit, borne in the sailing ship around the Horn, the year "the world rushed in". As a youth, he had enjoyed natural history in Connecticut and brought that sharing of enthusiasms with amateurs so important in scientific societies. Jepson relates the welcome reception Kellogg gave him as a young man⁴ on his first visit to the old Academy. The first of the many endemic species Kellogg described was the Channel Island mallow, *Lavatera assurgentiflora*. With a certain patriotism, he described the noble Washington Lily and with almost missionary zeal, the oracle oak, *Quercus morehus*. Occasionally, novelties slipped away from the Bay Region botanists to be first published by the Eastern Establishment and foreigners. Kellogg became almost militant and endeavored to publish "new species" more promptly through the Academy's *Bulletin*. He had seen John Lindley herald the Sierra sequoia in London before American scientific circles awoke.⁵ Kellogg, who lived 38 years in "the bosom of the urgent West", was *the* pioneer spirit.

TRANSCONTINENTAL AND STATE SURVEYS

Three enterprises brought California to the attention of botanists in the East and beyond. Locally, the California Geological Survey, commonly referred to as the "State Survey", staked out the limits of knowledge for the three kingdoms. The *Botany of California* in two volumes was especially important for the field work of William Henry Brewer, with his attention to detail and careful numbering of collections, and for his journal that documents his travels. From the surviving copies with their marginal notes and queries, it is evident how that important reference-work served California botanists.⁶ If you have not read Brewer's account, edited by Francis Farquhar under the title *Up and Down California*, you have a rewarding experience ahead.⁷ On one occasion John Muir wrote, "blessed Brewer of a thousand speeches and stories and merry ha-has."

Secondly, the Pacific Railroad Surveys carried out by the U.S. Army Corps of Engineers seeking a practicable route from the Mis-


ROOTS OF THE CALIFORNIA BOTANICAL SOCIETY

 International Phytogeographic Excursion Sept 1913	 California Botanical Society 12 Apr 1913	Pacific Division of A. A. A. S. 12 Apr 1913
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1910

Sierra Club 28 May 1892	 New England Botanical Club 1895	Harriman Alaska Expedition 1899
 New York Botanical Garden 1891	Stanford University 1891	 University of California Botanic Garden 1891
	 California Botanical Club 7 Mar 1891	

1890

San Diego Society of Natural History 1874	<i>Naturalists'</i> <i>Directory</i> 1877	New Orleans Cotton Centennial 1884	Bureau of Biological Survey 1885-1940
 Arnold Arboretum 1872	California College of Pharmacy 1872	San Francisco Microscopical Society 1872, 1893	

1870

University of California 1868	<i>American Naturalist</i> 1867	<i>Overland Monthly</i> 1868-1876	 Torrey Botanical Club 1867
	 Harvard University Gray Herbarium 1864		
Pacific RR Surveys 1853-1859		California Academy of Natural Sciences 1853	California Geological Survey 1853-1864

1850

FIG. 1. Roots of the California Botanical Society. Events, institutions, and organizations with botanical connections to the Society are identified by the leaf symbol. Publications are printed in italic. Dates represent the day or year in which an event occurred or was initiated or when an institution, organization, or journal was founded.

issippi River to the Pacific⁸ was another enterprise in the growth of California botanical knowledge, but the naturalists who accompanied the surveyors in their buckboard wagons and on horseback delivered collections to John Torrey in New York and Asa Gray at Harvard.

The essential reference herbarium delivered by Asa Gray to Harvard in 1864⁹ was the third event. The "Gray Herbarium" and the comprehensive library was to stand beside the Hooker Herbarium at Kew in calling for necessary visits by California students through the years.

TORREY BOTANICAL CLUB

Three years later (1867) and twelve years after the founding of the California Academy of Sciences, John Torrey, beloved by the botanical community, became the center piece for the Club that, against his wish, was to bear his name.¹⁰ There were 31 founding members. William Henry Leggett, a mainstay of its early years, began distributing a four-page monthly sheet in 1870 as a privately funded venture to which he gave the name "Bulletin of the Torrey Botanical Club". He admitted the Club was "rather informal and somewhat fluctuating". Prominent in the Club was George Thurber, editor and publisher of horticultural titles, who was instrumental in incorporating the Club. Today the Club of Leggett and Thurber flourishes as the oldest exclusively botanical society in America. Thurber's herbarium came to the Academy in 1893, only to be lost in the holocaust of 1906. John Strong Newberry, who had collected in California with the Pacific Railroad Survey, was president of the Club for ten years. Newberry's interest was fossil plants and he taught paleontology at Columbia College from 1866 to 1890.

American Naturalist AND *Overland Monthly*

How does the *American Naturalist* published in Salem, Massachusetts, feed the roots of a California society? Following the trans-continental railroads and the opening of the West, the signing of the Morrill Act in 1862, and the building of land-grant colleges, there followed a growing interest about the living things of this wilderness and wide-open spaces. Varied, informative, entertaining essays on the prairie dogs, pronghorns, burrowing owls, and locoweeds—life forms never seen in the East—appeared in the nineteen volumes of the *American Naturalist* of the late 19th century. Classes in academies and female seminaries were reading George Perkins Marsh's *Man and Nature*. To learn more about the West there was the *American Naturalist* with first-hand descriptions by Elliott Coues, Edward Palmer, William Henry Brewer, James Graham Cooper, and others. Cooper, for example, who had been an army surgeon with the Pacific

Railroad Surveys, wrote the ornithology volume for the California State Geological Survey—Brewer had collaborated with Asa Gray and Sereno Watson in the botany volume—after which Cooper moved to California.

The *American Naturalist* was founded in 1867 by four pupils of Louis Agassiz led by Frederic Ward Putnam (1839–1915), who in turn would be the teacher of David Starr Jordan. Putnam published on the fishes of Salem Harbor at 16 and became a most important ichthyologist of the 19th century. Described as “a wiry, nervous, black-haired, black-eyed, intense little fellow,” Putnam guided museums in Salem, Boston, and Cambridge, and for 25 years led the American Association for the Advancement of Sciences.¹¹ E. G. Conklin related in his “Early history of the *American Naturalist*” that, from its first printing of 250 copies, “Putnam was indefatigable in his work for the *Naturalist*.” Later in our story we shall see how Putnam also attended the birth of the *Naturalist's Directory*.

About this time, San Francisco's *Overland Monthly*, the “true pulse of a pioneer society”, as Franklin Walker¹² characterized it, was on sale in cities and towns. The cover of the first issue carried a grizzly bear, his feet planted on the iron rails, a snarling muzzle turned towards the oncoming westbound locomotive. He represented the independent spirit of the West. Anton Roman, its manager, had arrived in the gold mines in 1850, peddled books to the miners, then opened a bookstore in San Francisco in 1859. He published the *Overland Monthly* for eight years. Besides short stories—some gained lasting fame: for example, Bret Harte's *Luck of Roaring Camp* appearing in installments—scientific articles were featured. Andrew Jackson Grayson told about his Mexican jornadas; Josiah Whitney and Clarence King wrote their rockbound opinions; C. C. Parry,¹³ and separately, J. G. Lemmon, on their botanical excursions. In 1870 Anton Roman published Nicholas Bolander's *Catalogue of plants growing in the vicinity of San Francisco*.

BEHR, DAVIDSON, AND HARKNESS

A newcomer escaped from the German Revolution of 1848, and arrived in San Francisco in 1850 when wild columbines (*Aquilegia truncata*) grew on Telegraph Hill.¹⁴ Dr. Hans Herman Behr joined the Academy in 1854 and served as its vice president from 1864 to 1904. When the California College of Pharmacy opened in 1872 he began teaching botany and in 1884 published a *Synopsis of the Genera of Vascular Plants in the Vicinity of San Francisco, with an Attempt to arrange them according to evolutionary principles*,¹⁵ for his botany students. In 1896, he published his “Botanical reminiscences of San Francisco” in Jepson's *Erythea*. Hearty, generous, witty, Dr. Behr was popular in the Bohemian club, an association that Prof. Setchell later enjoyed.

Dr. Behr found a friend in George Davidson. Born in 1825 in Nottingham, England, Davidson spent his boyhood in Philadelphia. He entered the U.S. Coast Survey in 1845, preparing charts that guided the Gold Rush vessels that were soon to converge on the coast. He prepared successive editions of the *Coast Pilot*, known to the mariners as "Davidson's Bible". For sixty years he was the best known scientist on the Pacific Coast—a member of over forty scientific and learned societies. Fame is fickle. Davidson is not mentioned in the *Dictionary of Scientific Biography*. His 6.4 inch telescope in Lafayette Park, San Francisco, was the first observatory in the state, and he was pivotal in the history of the observatory funded by James Lick. His library was so rich that Robert Louis Stevenson was advised to check, on his visit to San Francisco, whether his wanted books on the South Pacific were in Davidson's library. They were. We do not think of this astronomer and geographer as a botanist, but both Asa Gray and Professor Greene commemorated Davidson for his plant collections.

Davidson was president of the California Academy of Sciences from 1871 to 1887. If you peruse the records of the Academy in that decade you will note two alliances: The Harkness-Brandegees vs. the Davidson-Behr alliance. Harvey Willson Harkness was born in 1821 in Pelham, Massachusetts, took his medical degree in 1847, and then fled to California where he practiced first at Bidwell's Bar.¹⁶ After his retirement in 1869, he devoted his years to fungi. Both M. C. Cooke and P. A. Saccardo named genera for Harkness, who described 108 new and old species of hypogeous fungi. He visited Sonoma County for truffles during the years Mrs. Curran (later Mrs. Katherine Brandegees) was botanizing there. David Starr Jordan characterized Harkness as "a physician of prominence", that he and Davidson "were vigorous and rather intolerant, a combination of qualities which was not rare in pioneer days."¹⁷ Davidson and Harkness were born of different temperaments and their discord was fueled by an Academy problem. Davidson's comrade, James Lick, had endowed the Academy handsomely and the funds were invested in a large office building on Market Street, where the Academy's museum occupied cramped quarters in the rear. Harkness, evidently joined by the Brandegees, wished to devote the entire building to the museum. Davidson proposed that an income property be developed and the Academy move to another site. He had been president of the Academy since 1871, but was defeated in 1887 by Dr. Harkness in a vote of 80 to 102. Tensions flared and by 1891 the supportive Brandegees commented that Dr. Harkness has been "sacrificing to the Academy's interest and advancement all his time, attention and energy." Soon after Harkness' victory, an argument arose with Dr. Behr at one of the Academy directors' meetings. Unable to stand the force of Behr's points, Harkness shouted, "Oh,

go to hell!" Behr answered politely, "After you, my dear sir." David Starr Jordan succeeded Harkness as president, but the rancor persisted. Within a decade, the three combatants had left the stage: first, Harkness in 1901, Behr in 1904, and finally, Davidson died in 1911 one year after he received an honorary LL.D. from the University of California.

CASSINO, ORCUTT, LEMMON, AND MERRIAM

Whereas the *American Naturalist* stimulated field biologists by its articles of discovery, the *Naturalist's Directory* matched collectors who might live on the opposite edges of the continent. For example, fern enthusiast John Gill Lemmon living in Sierra Valley might locate a fellow collector at the foot of the Adirondacks through the columns of the *Directory*. Although we associate the *Naturalist's Directory* with Samuel Edson Cassino, who first published it in book-form in 1877, it was Frederic W. Putnam, one of the founders of the *American Naturalist*, who initiated the idea of a directory. Putnam first listed 402 persons by "department of study" (Geology, etc.) and invited those and others to cooperate in a "Naturalist's Directory", as a feature of the *Proceedings of the Essex Institute* in 1865. Putnam managed and supported the "Directory" as part of his Salem Press, which published *American Naturalist*, until he disposed of the Directory to Cassino (1856–1937), then 22 years old. As a lad, Cassino had collected moths in company with entomologist A. S. Packard, author of a book on insects (also published by the Salem Press). *Cassino's Naturalist's Directory* as it came to be known appeared as his enterprise at intervals through the 30th edition (1936); under various managements it has continued to the present 44th edition (1985).¹⁸ The San Franciscans Kellogg, Behr, and Bolander appeared in the first Cassino *Naturalist's Directory* of 1877. Other Californians included Mrs. Ellwood Cooper of Santa Barbara and J. G. Cooper of Haywood, Alameda Co. By 1880, the "California" section of the *Directory* listed 140 names.

Daniel Cleveland came to San Diego in May 1869 at the age of 31 to carry on his law practice. In 1874, he was one of the founders of the San Diego Society of Natural History and soon was corresponding with Asa Gray, who named a delightfully fragrant sage, *Audibertia clevelandi*, which was collected in the mountains near Potrero east of San Diego. Parry visited Cleveland in 1882. Probably Parry and C. G. Pringle encouraged another San Diego naturalist, Charles Russell Orcutt, who was only 21, to launch a modest "popular monthly", the *West American Scientist*, in 1884. By 1890, his *Scientist* was identified on the cover as the "official organ" of the Society, selling for 10 cents per number or one dollar for the year. Its influence was wide indeed; contributors included Parry, Edward

Palmer, and T. D. A. Cockerell.¹⁹ San Diego, after San Francisco, continued as a Pacific Coast center of natural history into the 20th century, although Orcutt's *West American Scientist* remains a bibliographic relic.

The "good Doctor Parry" made influential friends. Among them were Leland Stanford and Charles Crocker, railroad builders who provided a pass for Parry and other botanists in the West. Parry likely spoke for John Gill Lemmon, who with his wife was thereby enabled to exhibit at the World's Industrial and Cotton Centennial Exposition that opened in New Orleans on 16 December 1884. The Southern Pacific Railroad had completed its route eastward from California to New Orleans in 1883. The booth at that Exposition may well have looked like a photograph labelled in Lemmon's hand "Lemmon Herbarium and its occupants", dated 23 June 1895²⁰ (Fig. 2). In this photograph, decorated with the *Darlingtonia* standing at the lower right, the portfolio on the floor, and behind the seated "occupants", is their precious curtained herbarium, the sheets resting as bolts of fabric in a department store. At the lower left we speculate that the *Botany of California* (in two volumes) or the *Pacific Railroad Reports* occupy the lowest shelf. Certainly Sara Allen Plummer Lemmon "energized his life", and was his helpmate in all his enterprises.²¹ Jepson knew and understood the Lemmons and in his characteristic esoteric way, fittingly labelled a *Lomatium* described from their collection the "Love Parsnip". The *Naturalist's Directory* of 1905 reads "Lemmon, Mrs. J. G., Artist and Explorer, Lemmon Herbarium, 5985 Telegraph Ave., Oakland, Calif. Bot., Cryptogams, Eth[nology]", concluding with an asterisk indicating that Cassino had heard from the person since the last *Directory* edition. The next entry, "Lemmon, Prof. John Gill . . ." concludes "Bot., Mic[roscopy], Forestry, Zool. C[ollection]" and the asterisk as above. Sara survived John and attended the natal meeting of the Society called by Jepson in 1913, but her name does not appear in the list of members; she died in 1923 at the age of 87.

Although Clinton Hart Merriam did not join the CBS, his "Life Zones" and the concepts it engendered continue to provoke discussions in the laboratory and around the campfire. Merriam knew the Adirondacks and then collected in the Yellowstone with the Hayden Survey when he was 16.²² His Bureau of Biological Survey, funded under various names, figured prominently in the West from 1885 to 1940. He organized the Death Valley Expedition of 1891 and its botanist, F. V. Coville, then 24, named the endemic poppy *Arctomecon merriami*. Merriam's Life Zones with "Lower Sonoran", "Upper Sonoran", etc., up to "Arctic-Alpine", were parts of the language that Merriam's boys adopted in the *North American Faunas*. Forty years after Merriam first proposed them, Jepson introduced his *Manual* with a review of "Life Zones". Merriam began



FIG. 2. The Lemmon Herbarium and its occupants (J. G. and S. P. Lemmon), Oakland, CA (23 Jun 1895).

mapping the Indian tribes of California and their uses of plants in 1904. He organized the Harriman Alaska Expedition, advised on its scientists, and finally edited its massive reports. He worked with his friend John Muir in conservation missions.

KATHERINE BRANDEGEE'S BOTANICAL CLUB

Competition is a growth-promoting substance for societies, as for American business. It is no misconception that the California Botanical Society had been delivered by Katherine Brandegee, M.D., assisted by Dr. Harkness in the "herbarium room" of the California Academy of Sciences on 7 March 1891. For the physicians' report read the journal *Zoe*,²³ itself brought into the world by the Brandegees in the 1890's. The Club had enrolled 99 charter members in the first month, including such names as Parish, Palmer, Cleveland,²⁴ Hasse, Sonne, Shockley, Carl Purdy, and John McLaren, Mrs. Ellwood Cooper of Santa Barbara,²⁵ and Mary Elizabeth Parsons—difficult to name a California enthusiast not in the Club. Prof. Dudley was president of the Club in 1893 and Parish of San Bernardino, vice president. Strong sentiments against Harkness and, by association, against Katherine Brandegee, are seen in Jepson's writings. In his admiring sketch of Edward Lee Greene published in 1918—Kate was still alive—Jepson related his first visit to the Academy when "an unkempt woman" with an "unpleasant voice" introduced Dr. Kellogg and Mr. Greene, whom she then labelled "a very wonderful man". Someday a biography of Willis Linn Jepson (Fig. 3)



FIG. 3. Willis Linn Jepson. Portrait by Peter Van Valkenburgh (Feb. 1927). "Telescope Peak; Panamint Range (11,000 ft.), looking toward Sierra Nevada."

will be written. A chapter may well be titled "Bold Kate, Jepson's 'Viper Parsnip' ".²⁶

SENATOR STANFORD'S DR. STILLMAN AND PROFESSOR DUDLEY

Just as during the 1850's, the 1890's were bustling meristemetic years for botany in the Bay Region. Growing points included Stan-

ford University, energized by President David Starr Jordan who brought William Russel Dudley to teach botany. Do not forget that Senator Stanford's private physician, Jacob Davis Babcock Stillman, had collected plants for John Torrey and that Stanford, on behalf of the Southern Pacific, befriended Parry with railroad passes for his botanizing junkets. Stanford had supported botany in small but important ways before Dudley came from Cornell. The Timothy Hopkins Seaside Laboratory, a "perfect paradise for the marine biologist" opened at Pacific Grove. Professor O. P. Jenkins²⁷ of Stanford was the director. Professor Setchell later found it a good collecting site for algae.

BRITTON-ABRAMS ALLIANCE

Far from California, but influencing its botanical future, was the founding of the New York Botanical Garden in 1891. The impact of its director and guiding spirit, Nathaniel Lord Britton, was to grant wide acceptance to the so-called American Code of Nomenclature that sought to enforce among botanists strict priority for the adoption of plant names. Professor LeRoy Abrams of Stanford, who succeeded Dudley, adopted the Brittonian code for his writings on the flora of the Pacific Coast. As David Keck has mentioned,²⁸ Jepson followed Harvard in adopting the policy of Kew in accepting plant names established by wide use among authors. Jepson viewed Abrams with his important *Illustrated Flora of the Pacific States* as a competitor and, in a way, this impelled Jepson to establish a California Botanical Society to advance his position of leadership in the botany of the state. Again, competition played its part here, as with Asa Gray versus Alphonso Wood in his bid for the market in introductory botany books for the East.

JOHN MUIR'S MEETING WITH JEPSON

John Muir's interest in learning plant affinities beyond the folk names was not acquired first in California—he had been botanizing in the savannahs of the South—but was fostered when he took the Sierras to heart. It was the Yosemite and the exploration of the great Tuolumne Canyon that he wrote about as early as 1871 in, to be sure, the *Overland Monthly*! Muir's journals demonstrate that he was acquainted with the botany of the *Pacific RR Reports*. In 1871, he wrote, "I made my camp in a grove of Williamson spruce"—that was an early name for the Mountain hemlock. There are dozens of such botanical identifications. Remember that Albert Kellogg, Galen Clark, and artist Billy Sims were with Muir as they camped on the way to Mount Whitney. He collected the alpine cinquefoil, named by Asa Gray *Ivesia muiri*, on Mount Hoffmann. In 1877, Muir was with Gray and Joseph Dalton Hooker on Mount Shasta. He was a

guest at the Bidwell home, Rancho Chico, when the majestic Hooker Oak that C. C. Parry wrote about in the *Overland Monthly*²⁹ was spreading its canopy. In 1888, Muir camped with Parry for more than a week on the shores of Lake Tahoe. Afterwards, Muir would recall, "I had him all to myself—precious memories."

One of the roots of this Society was Jepson's meeting with John Muir in the founding of the Sierra Club. When and where Jepson first met Muir, I cannot say, but on 28 May 1892, they joined Joachim Henry Senger, a professor of German, William Dallam Armes,³⁰ who taught American literature at Berkeley, and William E. Colby,³¹ who was later prominent in the Sierra Club, at the office of attorney Warren Olney in San Francisco, to draft the articles of incorporation of the Sierra Club. Professor Armes, a bachelor, had been teaching at Berkeley since 1882 and was living in the Faculty Club. Later, Armes edited Joseph LeConte's *Autobiography* (1903) and published a critique of More's *Utopia* (1912). Clearly, the two Berkeley professors were congenial friends of Jepson.

HARRIMAN ALASKA EXPEDITION, FARLOW AND SETCHELL

Alaska took the front stage in 1899 with businessman Edward H. Harriman in the lead role and a supporting cast of 25 scientists. The Harriman Alaska Expedition was a success that produced multi-volumed reports edited by Merriam. The only University of California faculty man to accompany the Expedition was William Ritter, although Jepson and Setchell met the Harriman party that summer.

William Albert Setchell had arrived in Berkeley to succeed Professor E. L. Greene in 1895. That year, the New England Botanical Club had been founded by Setchell's mentor, W. G. Farlow, and six associates and in four years the Club numbered 46 gentlemen "of leisure but not of idleness".³² Farlow had been an assistant to Asa Gray in 1871 and later left his stroma of *mycologia* and an endowment to Harvard for cryptogamic botany, with the stipulation that "no part thereof shall be used to pay for lectures or instruction of any kind."³³ Setchell has related how a small separate expedition to Alaska had been planned in 1898, evidently while the Harriman Expedition was being planned.³⁴ Four of the members of the University of California had made reasonably definite arrangements to attempt some limited botanical exploration in the same general field, and especially had set their eyes on the region of the Island of Unalaska, at the southeastern corner of the Bering Sea. Besides Setchell and Jepson, then Assistant Professor of Botany, Anstruther Abercrombie Lawson, who had graduated in botany in 1897, and Loren Edward Hunt, Instructor in Civil Engineering, participated in the expedition. Jepson recorded in his Field Book that Hunt was "going along as supercargo and handy member of the party." Jepson

noted that the Harriman Expedition arrived at Unalaska 12–13 July 1899 and on that occasion he met several members of the Expedition including Merriam, Coville, Muir, and John Burroughs. Anstruther Lawson later became Professor of Botany at University of Sydney, and studied plant embryogeny, *Psilotum*, and gymnosperms. He was at Stanford from 1900 to 1906 where he wrote the “Life history of Sequoia”. Anstruther Lawson was brother of the witty combative geologist of Berkeley, Andrew Cowper Lawson.

JEPSON’S CALIFORNIA BOTANICAL SOCIETY

Jepson confided in his 1938 anniversary address to the CBS that the “idea of a Society was definitely conceived in the year 1902”.³⁵ It is easy to see how the stimulating meetings with outside scientists and the comradeship that then had existed with Setchell would have given rise to the merit of such a Society, but then Jepson added, “some one may note the lapse between that date and the year 1913 when the Society was founded.” He then suggested that a certain disassociation of the Stanford and Berkeley botanists may have been responsible for the delay. I suggest a certain competitive spirit that existed between the botanists of Stanford and Berkeley, and differences, for example, in the adoption of opposing codes of nomenclature as practiced by Abrams and Jepson, may have dissociated them. Then, too, the conspicuous vigor of the California Botanical Club and its associates in San Francisco, all contributed to Jepson’s compelling interest in founding the CBS directed from Berkeley.

Two Berkeley faculty members were prominently attending the birth of the Society. William Frederic Badé was temporary chairman of that founding meeting of the Society on 12 April 1913, and then was elected second vice president. Badé, an archeologist, linguist, and literary executor of John Muir had edited Muir’s letters.³⁶ He was a distinguished figure. Curiously, Jepson did not mention Badé in his Annual Dinner address of 1938, although he had died only two years before. By contrast and in lengthy prose, Jepson praised Cornelius Beach Bradley, professor of rhetoric at Berkeley who had missed being a full-time botanist, in Jepson’s words, “by only a narrow margin.”

Then on the same April day in 1913 on which the Society was being born at the Oakland Public Museum, another meeting was under way on the Berkeley campus. In preparation for the coming Pan Pacific International Exposition of 1915, the original AAAS founded and based in the East determined that it should be represented by a *Pacific Division*. Botanist Daniel Trembly MacDougal prompted that action. A committee of twenty scientists met to inaugurate a Pacific Division with W. W. Campbell in the chair.³⁷ Some of the other Berkeley faculty present were E. W. Hilgard, C.

A. Kofoid, A. L. Kroeber, A. C. Lawson, Ritter and Setchell. Professor Setchell was enrolled a charter member of the CBS, although he evidently was not present at the Oakland meeting.

INTERNATIONAL PHYTOGEOGRAPHICAL EXCURSION

The International Phytogeographical Excursion (IPE) of 1913, when European and Eastern botanists visited California after field trips in the Rocky Mountains and Crater Lake, was another root nourishing the growth of botany in the Bay Region.³⁸ Although the IPE took place five months after the founding of the Society, preparations had been going forward before the April meeting in Oakland. Botanists from Amsterdam, Copenhagen, Berlin, Munich, Zurich, and Cambridge, England, met their colleagues from Berkeley, San Francisco, and Stanford, later to be joined by MacDougal from Tucson and Samuel Bonsall Parish from San Bernardino. A new language of flowers was heard when the excursionists discovered that "Sail-ix" grows in America, "Sall-ix" in Europe. Whatever animus may have separated faculties was lost for the days the excursionists tramped California's chaparral and shared their experiences. The IPE was a high point for Jepson. He related some details in the first issue of *Madroño*, which appeared three years after the founding of the Society.

On Friday 12 September 1913, Professor Jepson presided at the dinner for the IPE. His closing words were:

"Now there arises a school of botanists, the plant ecologists, who are leading us back to the fields and woods, taking with them the experience of all other schools, and in addition making important use of the observations of the old-time naturalists. California is a glorious field for such work, and we welcome them here to help us appreciate our own flora, and to help Californians to an appreciation of it."

Montesquieu was right: Jepson shaped the Society but the Society in turn shaped Jepson's dream. On one of my 5 × 8 half-sheets for 15 March 1937, I wrote, "I learn tonight of a boyhood dream or aircastle, which Dr. Jepson himself now says was 'preposterous.'³⁹ In Vaca Valley, his boyhood home, stood a two-story brick building occupied by a small college dating from the Gold Rush days with something of a classic demeanor, a courtly flavor. This stood on a low hill with creek bed beside it deeply filled with rich alluvium. As a lad he envisioned devoting the structure to an herbarium and of surrounding it with a botanic garden. As a boy he did not have money to think of such a reality but he had the 'desire'."

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Tulanians: Milton G. Scheuermann, Professor of Architecture, and Dolores Gunning, Department Secretary. First and last, my wife Nesta.

NOTES

A complementary essay to this subject is by J. Ewan (San Francisco as a mecca for 19th century naturalists with a roster of biographical references to visitors and residents, *In Century of progress in the natural sciences, 1853–1953*. pp. 1–63. California Academy of Sciences, San Francisco, 1955), hereinafter cited as *Century*.

1. Carlin, Eva V., ed. 1898. A Berkeley year. A sheaf of nature essays. pp. 61–64. Women's Auxiliary of the First Unitarian Church, Berkeley.
2. William S. Ferguson, Greek Imperialism, 1913, quoted in: Charles P. Curtis, Jr. and Ferris Greenslet. 1962. *Practical Cogitator*. ed. 3. New York. p. 134.
3. G. M. Trevelyan, *ibid*. p. 131.
4. Carew, Harold D. 1928. High priest of Flora. A glance at the life and works of Willis Linn Jepson, California's foremost botanist. *Touring Topics* 20(12):32–34, 50. p. 31.
5. Ewan, J. 1973. William Lobb, plant hunter for Veitch and messenger of the Big Tree. *Univ. Calif. Publ. Bot.* 67:1–36. p. 7. For the "smouldering resentment" of California botanists see: A. H. Dupree. 1959. Asa Gray. Harvard Univ. Press. pp. 395–396.
6. See W. L. Jepson (*Flora Calif.* 2:6. 1936). Volume 1 of *Botany California* (1876) was reprinted with additions in 1880, the year vol. 2 was published in a smaller printing because of reduced funding.
7. Yale Univ. Press. 1930. Jepson assisted Farquhar with plant identifications. For a charming vignette of Brewer, "omnivorous devourer of facts in every field", with a "tentacular mind", see: Rudolph Schevill (*Recollections of a golden age*. Pittsburgh, pp. 174–175, 1985). Ian Jackson provided this trail sign.
8. For a consummate analysis see: Max Meisel. 1929. *Bibliography of American Natural History*. New York. 3:189–220; and for critical commentary: I. M. Johnston. 1943. *J. Arnold Arbor.* 24:237–242.
9. Dupree, A. Hunter. *op. cit.* pp. 327–328. John Torrey was present at the Harvard occasion. The herbarium contained "at least 200,000 specimens", valued especially for the types.
10. Barnhart, John H. 1918. Historical sketch of the Torrey Botanical Club. *Mem. Torrey Bot. Club* 17:12–21.
11. Conklin, E. G. 1944. Early history of the American Naturalist. *Amer. Naturalist* 78:29–37; Ralph W. Dexter. 1982. F. W. Putnam as secretary of the A.A.A.S. (1873–1898). *Essex Inst. Historical Collections* 118:106–118, especially 109.
12. Walker, Franklin. 1939. San Francisco's literary frontier. Knopf, New York. pp. 256–283, especially 279–280.
13. See: J. Ewan. 1950. Rocky Mountain Naturalists. Univ. Denver Press. pp. 34–44. Portrait and suppl. refs. *In* J. and N. Ewan. 1981. *Biographical dictionary of Rocky Mountain naturalists*. Utrecht. pp. 168–169.
14. *Zoë* 2:3. 1891.
15. *Century*, pp. 12 and 43. A long overdue biography of Behr, a "Forty-eighter" and friend of Alice Eastwood, would profile a half century of California history.
16. T. S. Brandegee's biography of Harkness (*Zoë* 2:1–2 and portrait, 1891) was clearly an apology that appeared ten years before the death of Harkness.
17. *Century*, p. 37.
18. 44th edition of the *Naturalist's Directory* (Flora and Fauna Pubs., Gainesville, FL, 1985) includes a portrait of S. E. Cassino (p. vi) and the first history of this important chapter in American natural history by Ralph W. Dexter (pp. 1–7) and additional notes by Ross and Mary Arnett. References kindly supplied by Dale Johnson (MO).
19. For references on Theodore Dru Alison Cockerell (1866–1948) see: J. Ewan and

- N. Ewan. 1981. *op. cit.* pp. 44–45. Also see: W. A. Weber. 1976. Theodore D. A. Cockerell. Colorado Assoc. Univ. Press. Most recent account of C. R. Orcutt (1864–1929) by Helen DuShane (Baja Calif. Travel Series, 23, Dawson's, Los Angeles, 1971) extends Jepson's account (Madroño 1:273–274, 1929). Lee W. Lenz (Marcus E. Jones. Rancho Santa Ana Botanic Garden, Claremont, CA. pp. 52–57, 1986) reviews the Orcutt-Parry-Pringle-Jones episode.
20. J. G. Lemmon was certainly the author of the anonymous "Catalogue of the plants and paintings of the Lemmon Herbarium" that appeared in Charles B. Turrill (Catalogue of the products of California exhibited by the Southern Pacific Company . . . Nov. 10, 1885–April 1, 1886. New Orleans, pp. 55–62, 1886). Jepson annotated this unpublished record (Fig. 2) as an "interesting photograph because it tells so much of what Lemmons were personally and botanically" and that it was communicated by Dr. Rimo Bacigalupi, ca. Sep 1932. For Lemmon references see Century, pp. 23–24, 54, Ewan, *op. cit.* (1981, p. 132) and F. S. Crosswhite (Desert Plants 1:12–21 and portraits, 1979).
 21. Jepson, W. L. 1946. Dict. Amer. Biog. 11:162; J. Ewan. 1944. Amer. Midl. Naturalist 32:513–518.
 22. Clinton Hart Merriam (1855–1942) was the "central figure in a dynamic era connecting the pioneer period of exploration with the present time of experimentation and interpretation" (Wilfred H. Osgood. 1945. Biogr. Mem. Natl. Acad. Sci. USA. 24:1–57, with bibliog. of his publs.). "Merriam, Vernon Bailey, and the cyclone trap fleshed out mammalogy as a science in America" (p. 9).
 23. Zoë 2:93–96. 1891; Century, pp. 36–37. Alice Eastwood presided over the California Botanical Club for more than sixty years from her first meeting of 26 Apr 1892 (Leaf. W. Bot. 7:59, 1953). A useful account of K. Brandegee is in: Notable Amer. Women 1:228–229, 1971.
 24. Daniel Cleveland (1838–1929) and associates are described in: Elizabeth C. MacPhail. 1976. Kate Sessions, pioneer horticulturist. San Diego Hort. Soc., San Diego. pp. 44 and 69; also see: Century, pp. 37 and 46.
 25. Sarah Paxen Moore Cooper (died 1908) married Ellwood Cooper (1829–1918) in August, 1853 (*teste* J. H. Barnhart). Cooper was a pioneer in eucalyptus cultivation in California. His friend Lorenzo Gordin Yates (1837–1909) who came to Santa Barbara in 1881, became president of the Santa Barbara Natural History society that was founded in 1876 (Charles L. Camp. 1963. J. Soc. Bibliogr. Nat. Hist. 4:178–193). Also see: Clifton F. Smith. 1976. Flora of the Santa Barbara Region, California. Santa Barbara Mus. Nat. Hist., Santa Barbara, pp. 42 and 59. He tells me (litt. 1972) that J. G. Lemmon and Henry Bolander visited the Cooper ranch near Goleta.
 26. Jepson portrayed K. Brandegee (Newman Hall Review 1:24, 1918). Type of "Viper parsnip" (*Leptotaenia anomala* Coult. & Rose) was taken by Katherine Curran near Carbondale, Amador Co., CA (W. L. Jepson, Flora Calif. 2:634, 1936). Other accounts: Century, p. 32–33; F. S. and C. D. Crosswhite (Desert Plants 7:128–139, 158–162, and portraits, 1985).
 27. Zoë 4:58–63 and pl. 26. 1893. Oliver Peebles Jenkins (1850–1935), physiologist and ichthyologist was noticed in: David Starr Jordan. 1922. Days of a man. New York. 1:399–400.
 28. Keck, D. D. 1948. Place of Willis Linn Jepson in California botany. Madroño 9:223–228.
 29. Parry, C. C. 1888. Rancho Chico. Overland Monthly ser. 2. 11:561–576. Photographs of "Sir Joseph Hooker Oak" on p. 565 and in: Rockwell D. Hunt. 1942. John Bidwell. Caldwell, Idaho. opp. p. 273. Parry is noticed on pp. 209, 211–212, 278–279.
 30. "Organization and early conservation activities of the [Sierra] Club" included W. Olney, Joseph LeConte, J. H. Senger, W. D. Armes, and C. B. Bradley, according to W. F. Badé (Life and Letters of John Muir, Boston, 2:256, 1924), but Jepson was not mentioned. Also, Holway R. Jones (John Muir and the Sierra Club, Sierra Club, San Francisco, pp. 7–9, 1965) did not mention Jepson. Jepson,

however, was present at the meeting of 28 May 1892, according to Linnie Marsh Wolfe (John of the mountains: the unpublished journals of John Muir, New York, p. 299, 1938; and Son of the Wilderness: the Life of John Muir, New York, pp. 254 and 360, 1947). Professor Senger taught German at Berkeley 1886–1913 and died in 1926. “Billy” Armes was evidently a popular professor, judging by comment of Loye Miller (Lifelong Boyhood. Berkeley, p. 58, 1950). Armes died in 1926.

31. William E. Colby (1875–1964) a lawyer and native of Benicia, California, joined the Sierra Club in 1898 and was active (president 1917–1919) to his death. Warren Olney (1870–1939), a lawyer and native of San Francisco, is quoted by Badé (*op. cit.* 2:376–377). Mrs. Edward T. Parsons, Muir’s friend, of that letter, was a charter member of the California Botanical Society.
32. Williams, E. F. 1899. New England Botanical Club. *Rhodora* 1:37–39.
33. Setchell, W. A. 1927. William Gilson Farlow. *Biogr. Mem. Natl. Acad. Sci. USA*. 21(4):1–22. portrait.
34. Setchell, W. A. 1907. *Univ. Calif. Publ. Bot.* 2:309–311. Note on A. A. Lawson (1870–1926) occurs in: Francis E. Vaughan. 1970. Andrew C. Lawson. Glendale, CA. pp. 38–39. Loren Edward Hunt, who contributed photographs to Jepson’s *Silva of California*, accompanied him on a field trip to Blue Lakes, Lake Co., 16 Jul 1897, when the type of *Godetia amoena* f. *huntiana* Jeps. was collected.
35. Jepson, W. L. 1938. *Viae felicitatis: the beginning years of the California Botanical Society*. *Madroño* 4:276–286. see p. 282.
36. William Frederic Badé (1871–1936), archeologist, professor, and acting president of the Pacific Theological Seminary, later Pacific School of Religion, Bancroft Way, Berkeley, and outdoorsman, “one of the most able and devoted preservationists” (James Mitchell Clarke. 1980. *Life and adventures of John Muir*. Sierra Club, San Francisco. pp. 304 and 320). Also see C. C. McCown in: *Dict. Amer. Biog. suppl.* 2, 1958. Cornelius Beach Bradley (1843–1936) was a missionary and professor of English, UC Berkeley (1882–1911).
37. Robert C. Miller (*Science* 108:220–221, 1948) lists members of the committee.
38. *Madroño* (1:12–18, 1916) includes a photograph of 14 identified participants taken at Mariposa Grove of Big Trees. Also see G. E. Nichols (*International Phytogeographic Excursion in America*. *Torreyia* 14:55–64, 1914); A. G. Tansley (*New Phytol.* 12:322–336, 1914; and 13:30–41. 83–92, 1914); the F. E. Clements records in *Univ. Wyoming archives*, Laramie; and a note by Paul B. Sears (*Plant Ecology*. In J. Ewan, *Short history of botany in the United States*, Hafner, New York, pp. 130–131, 1969).
39. During my four years with Jepson (see his *Flora Calif.* 2:10, 1936) I recorded conversations and events on half-sheets.

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ANNOUNCEMENT

JOINT ANNUAL MEETING OF AIBS, ASPT, BSA, AND ESA

9–13 August 1987, Ohio State University

Two symposia in botany will be presented this year: one on the Generic Concept, and one on the Reproductive Ecology of Aquatic Angiosperms.

INFLORESCENCE ARCHITECTURE OF *EUCNIDE* (LOASACEAE)

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ABSTRACT

Terminal inflorescences and axillary flowers have been reported in recent revisions of *Eucnide* (Loasaceae). Developmental studies show, however, that axillary flowers are not present. All flowers are terminal: the initial shoot axis terminates in a flower, and lateral branches that terminate in flowers after producing only one or two leaves arise from the distal nodes of each initial and renewal axis. The branching pattern in the inflorescence region of each axis is complicated by the apparent displacement of subtending leaves outward onto lateral floral branches during their extension. Renewal axes that first arise in the nodes subjacent to lateral floral axes reiterate the pattern of the initial axis.

Recent systematic treatments of *Eucnide* (Loasaceae) have largely underestimated the architecture of the inflorescence. Waterfall (1959) used floral position to separate "two natural, but somewhat intergrading series in the genus." His first series, comprised of *E. bartonioides*, *E. xylinea*, and *E. urens*, was characterized by solitary flowers in leaf axils. The second series had "terminal inflorescences more or less developed." The most recent revision by Thompson and Ernst (1967) distinguished three sections in *Eucnide* (including *Sympetaleia* at the sectional level; Waterfall did not consider *Sympetaleia* to be congeneric with *Eucnide*). Thompson and Ernst did not retain the informal division based on floral position proposed by Waterfall, and inflorescence data does not appear to have had a major role in their sectional circumscriptions. They observed terminal inflorescences of a few flowers in most species and noted axillary flowers in more than half of the species. The only inflorescence data given for the new species *E. durangensis* (Thompson and Powell 1981) was in the Latin description: "*Inflorescence pauci-vel multiflorae*".

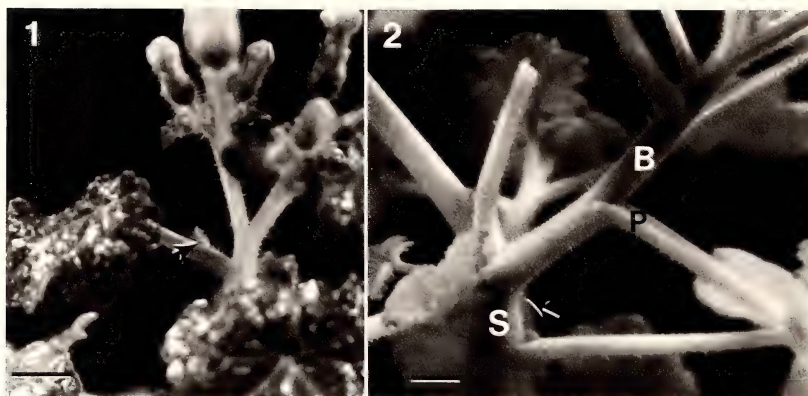
My investigations show that our current knowledge of inflorescence morphology of *Eucnide* is oversimplified. The purpose of this paper is to clarify the inflorescence architecture of *Eucnide* by placing it in the context of whole plant morphology and development.

MATERIALS AND METHODS

Eucnide bartonioides (seven plants), *E. cordata* (four plants), *E. hirta* (two plants), and *E. lobata* (three plants) of Thompson and Ernst's sect. *Eucnide* and *E. aurea* (three plants) of sect. *Sympetaleia*

TABLE 1. PERTINENT COLLECTIONS OF *Eucnide* USED FOR THIS INVESTIGATION.
 * = collections that were sources of seeds for glasshouse populations.

Species	Collection
Sect. <i>Eucnide</i>	
<i>E. bartonioides</i> Zucc.	USA, Texas: Big Bend National Park, 26 Jun 1962, <i>Thompson and Ernst</i> 3283 (LA)*. MEX, Tamaulipas: Jaumave, 25 Nov 1962, <i>Moran</i> 10031 (LA, UC); Nuevo Leon: Cuesta de Mamilique, 14 Aug 1942, <i>Gentry</i> 6729 (UC).
<i>E. cordata</i> (Kell.) Kell. ex Curran	MEX, Baja California Sur: La Paz, 29 Dec 1958, <i>Porter</i> 106 (LA); Sierra de la Gigantea, 9 Nov 1961, <i>Carter</i> 4278 (UC); Isla Monserrate, 27 Mar 1977, <i>Cody</i> (<i>Thompson</i> 3829 seed collection) (LA)*.
<i>E. durangensis</i> Thompson & Powell	MEX, Durango: Gomez Palacio, 25 Mar 1973, <i>Johnston, Wendt, and Chiang</i> 10417 (LA); Torreon, 14 Aug 1973, <i>Henrickson</i> 12405 (LA).
<i>E. floribunda</i> S. Wats.	MEX, Coahuila: Cuatro Ciénegas, 10 Jun 1968, <i>Lehto, Keil, and Pinkava</i> 5360 (LA); 4 Apr 1969, <i>LaBounty, Lehto, and Pinkava</i> 5927 (LA); Las Delicias, 12 Aug 1973, <i>Henrickson</i> 12240 (LA).
<i>E. grandiflora</i> (Groenl.) Rose	MEX, Oaxaca: Tomellin Canyon, 17 May 1894, <i>Pringle</i> 4645 (GH); Jayacatlan, 4 Nov 1973, <i>Breedlove</i> 35885 (RSA); Teotitlan del Carmen, 22 Aug 1975, <i>Webster, Armbruster, and Holstein</i> 20036 (GH).
<i>E. hirta</i> (G. Don) Thomp- son & Ernst	MEX, Jalisco: San Cristobal de la Barranca, 11 Nov 1962, <i>McVaugh</i> 22140 (NY, LL); Tizapan, 30 Jun 1957, <i>McVaugh</i> 15108 (<i>Thompson</i> 3319 seed collection)*; Veracruz: Cerca de Puente Nacional, 13 Jan 1973, <i>Hernandez, Dorantes, and Dorantes</i> 1819 (NY).
<i>E. hypomalaca</i> Standl.	MEX, Chihuahua: Batopilas, 15 Apr 1948, <i>Hewitt</i> 272 (GH); Chiapas: Chiapa de Corzo, 24 Feb 1973, <i>Breedlove</i> 33828 (RSA).
<i>E. lobata</i> (Hook.) A. Gray	MEX, Hidalgo: Barranca de Toliman, 27 Nov 1962, <i>Moran</i> 10048 (LA); Nuevo Leon: Monterrey, 10 Aug 1959, <i>Waterfall</i> 15324 (F) (<i>Thompson</i> 3298-6 seed collection) (LA)*; Coahuila: Carmen Pass, 6 Aug 1978, <i>Fryxell</i> 3023 (ASU)*.
Sect. <i>Sympetaleia</i>	
<i>E. aurea</i> (A. Gray) Thompson & Ernst	MEX, Baja California: Sierra de la Gigantea, 25 Nov 1953, <i>Carter and Kellogg</i> 3266 (UC); Isla Carmen, 10 Mar 1960, <i>Carter and Ferris</i> 3710 (UC); Idlefonas Island, 2 Apr 1962, <i>Moran</i> 9056 (ASU)*.
<i>E. rupestris</i> (Baill.) Thompson & Ernst	MEX, Baja California: Mexicali, 22 Feb 1960, <i>Raven</i> 14802 (LA); San Estaban Island, 22 Mar 1962, <i>Moran</i> 8858 (LA); Bahia de Los Angeles, 26 Feb 1963, <i>Thorne and Henrickson</i> 32694 (LA).
<i>E. tenella</i> (I. M. Johnst.) Thompson & Ernst	MEX, Baja California Sur: Mission Los Delores, 5 Dec 1951, <i>Wiggins, Carter, and Ernst</i> 260 (LA); Sierra de la Gigantea, 31 Oct 1971, <i>Moran</i> 18845 (UC); Sierra de la Gigantea, 5 Nov 1971, <i>Moran</i> 19017 (UC).
Sect. <i>Mentzeliopsis</i>	
<i>E. urens</i> Parry	USA, California: Whipple Mountains, 20 Mar 1936, <i>Clary</i> 2580 (JEPS); near Death Valley National Monument, 17 Mar 1984, <i>Hufford</i> 1114 (UC); Trona, 18 Mar 1984, <i>Hufford</i> 1116 (UC); MEX, Baja California: Okie Landing, 4 May 1966, <i>Moran</i> 13124 (UC).



FIGS. 1-2. Recauscence in *Eucnide*. FIG. 1. Axillary bud (arrow) displaced onto petiole of leaf in *E. aurea*. FIG. 2. After extension of the lateral branch, the subtending leaf (P indicates the petiole of the leaf) appears to be inserted on the lateral branch (B) derived from its axil because of extension of the common basal portion of both leaf and branch. Arrow indicates position of insertion of the leaf (P) on the axis (S) where it arose in *E. cordata*. Scale bars equal 5 mm.

were grown under glasshouse conditions in Berkeley, California. *Eucnide urens*, comprising sect. *Mentzeliopsis*, was examined under natural conditions (Table 1). I examined herbarium specimens of all species, except *E. xylinea* C. H. Muller. Collection data for pertinent herbarium specimens and sources of seeds for glasshouse populations are given in Table 1.

The term inflorescence is used in this paper in the sense of Steenis (1963), who defined it as "the specialized fertile part(s) of an individual plant which post anthesis does (do) not participate in the vegetative extension of the individual', and is hence either shed or withering away."

RESULTS

All species of *Eucnide* are perennial. The shoot system is sympodial; each shoot axis eventually terminates in a flower. A slight concaulescence (adnation of the pedicel of the terminal flower with the uppermost lateral branch, Troll 1964) is common among all of the species, although it is not a consistent feature of all individuals of any species. Plants grown under glasshouse conditions develop approximately five to ten leaves following the cotyledons and before terminal flower formation. The distal-most leaves of each axis are recaulescent (sensu Troll 1964, see also Kuijt 1981) with their axillary buds. Recauscence implies that an axillary bud is somewhat displaced onto the petiole of the subtending leaf (Fig. 1; this con-

dition is also called epipetioly, Dickinson 1978). When the axillary bud begins extension the basal region common to the subtending leaf and axillary bud also begins outgrowth. At full extension of a lateral floral branch, the 'subtending leaf' appears to be inserted on the lateral axis rather than on the axis on which it was produced (Fig. 2).

Sect. EUCNIDE. In glasshouse populations of *E. bartonioides*, *E. hirta*, and *E. lobata*, the three leaves and axillary buds subjacent to the terminal flower are recaulescent (Figs. 3, 4). Of these three uppermost nodes, lateral floral axes usually arise in the axils of the two distal leaves (forming a dichasial inflorescence, Figs. 3, 4), although only the uppermost node may form a lateral floral axis (a monochasial inflorescence). The terminal flower and either the monochasial or dichasial lateral floral axes form the inflorescence of each shoot axis. Lateral floral axes in these species do not undergo extensive internodal elongation. Internodes of these lateral floral axes elongate only as flowers begin to mature and then most of the elongation is in the pedicel. Each lateral floral axis usually produces two leaves (Fig. 5) or may form only one leaf (Fig. 6) and a terminal flower. Each leaf of this primary lateral axis becomes recaulescent with the bud in its axil. Each of these axillary buds (secondary lateral axes) repeats this pattern of producing one or two leaves (each becoming recaulescent with its axillary bud) and a terminal flower (Figs. 5, 6). The lateral floral axes may be either dichasial (Fig. 5) or monochasial (Fig. 6). Some herbarium specimens show that inflorescence development changed from one condition to the other during ontogeny. Lateral floral axes were not observed (in neither glasshouse populations nor on herbarium specimens) to convert back to vegetative growth (i.e., back to production of more than two leaves before terminal flower formation). This pattern of inflorescence architecture appears to be common to all species of section *Eucnide* (except *E. xylinea*, which was unavailable, and *E. cordata*, which is discussed below) as ascertainable from examination of herbarium specimens (Table 1).

Leaf form undergoes a gradual transformation in the transition to the flowering region. Leaf laminae with a lobate margin and a cordate base are produced in the vegetative portion of the plant. At the few nodes proximal to the inflorescence region, where the internodes do not extensively elongate, the leaves are smaller. Leaves lose regularly lobed margins and cordate bases with transition into the region of lateral floral axes. Leaves on some primary, secondary, and tertiary axes of the inflorescence often occur as tiny, lanceolate bracts.

The recaulescent 'node' (involving leaf and axillary bud) on the main shoot, which was not immediately floral, is the location of the first renewal shoot (Figs. 3, 4) or innovation shoot (sensu Weberling



FIGS. 3-10. Renewal growth and inflorescence architecture of *Eucnide*. FIG. 3. Monochasial renewal, one renewal branch arises from the node proximal to the lateral flowering axes. FIG. 4. Dichasial renewal, vegetative branches arise from the two nodes proximal to the lateral flowering axes. FIG. 5. Flower and leaf positions on dichasial floral axes that would be located at positions indicated by solid arrows in Figs. 3 and 4. Terminal flowers of successive lateral axes are indicated. FIG. 6. Flower and leaf positions on monochasial floral axes that would be located at positions indicated by solid arrows in Figs. 3 and 4. Terminal flowers of successive lateral axes are indicated. FIG. 7. Shoot terminus of *E. cordata* prior to secondary branching of the inflorescence. FIG. 8. Architecture of *E. cordata* inflorescence. Terminal flowers of primary, secondary, and tertiary axes are indicated for one of the three floral branches. FIG. 9. Architecture of shoot system of *E. tenella*, showing dichasial branching on left side and monochasial branching on right. FIG. 10. Architecture of inflorescence of *E. urens*, showing displacement (concaulescence) of terminal flowers toward subjacent lateral branches. A = terminal flower, B = floral branch, C = vegetative branch, D = leaf produced by axis on which it is inserted, E = leaf produced by axis

1983). The subjacent node at which there is usually no recaulescence has an axillary bud that subsequently begins renewal growth. The sympodial growth pattern appears to be primarily, although not strictly, dichasial (Fig. 4). Monochasial renewal (Fig. 3; especially in *E. lobata*) and also pleiochasial renewal growth (usually three branches in *E. bartonioides*) are common. Following transition to flowering on a renewal axis, buds in leaf axils (although these leaves have withered) of the previous axis also will begin growth. Outgrowth of buds along this axis is basitonic (i.e., beginning near the base of an axis with acropetal progression). The first few internodes of renewal axes elongate. As an axis nears flowering, internodes remain largely unextended. Each renewal shoot produces only five to ten leaves before forming a terminal flower. The inflorescence of any shoot axis in *Eucnide* may be considered to be the region above the uppermost renewal branch because this portion of the plant usually dries and withers after flowering (it does not contribute to further vegetative extension). Renewal growth patterns were difficult to determine for species that were not grown under glasshouse conditions because herbarium specimens seldom have enough of the plant for evaluation.

Eucnide cordata differs from all species described above. It has longer renewal shoots that produce more leaves before conversion to flowering. The internode, between the lowest node with a leaf that becomes recaulescent and a nonrecaulescent leaf, becomes elongated when flowering begins. The next distal internode also becomes quite elongated and effectively segregates an inflorescence region that is more distinct than in the other species of sect. *Eucnide*. These penultimate internodes in the other species remain compact.

The basic architectural pattern of the flowering region in *E. cordata* is similar to that described above for other species in sect. *Eucnide*; however, there are some distinctions. Three lateral floral axes (Fig. 7) are produced on the initial axis and each renewal branch, rather than the two most commonly produced in *Eucnide* (Figs. 3, 4). Each of these primary lateral axes (Fig. 8) produces two or occasionally more leaves and a terminal flower. The leaf subtending a primary lateral axis becomes recaulescent as is common in *Eucnide*. The first leaf produced by a primary floral axis often remains at nearly the same level as the subtending leaf because the internode between them does not elongate. An axillary bud may or may not form in association with this first leaf. If an axillary bud does form it is floral

←

subjacent to the one on which it is inserted (recaulescence). T = terminal flower, 1° = flower of primary, 2° = flower of secondary, 3° = flower of tertiary, and 4° = flower of quaternary floral branches.

(a secondary floral axis). This secondary floral axis produces two leaves, but only the uppermost produces an axillary bud that is floral (a tertiary lateral axis). The uppermost leaf of the primary lateral axis also has an axillary bud. This again becomes a secondary floral axis that produces two leaves, only one of which subtends a floral bud (another tertiary lateral axis). Each tertiary axis present (there may be two associated with each primary lateral axis) produces two leaves (one of which has an axillary bud) and a flower. Leaves on these floral axes, which subtend axillary buds, usually become recalescent with that lateral axis when the axis begins growth. The lateral axes in the inflorescence region of *E. cordata* have greater internodal growth than is common among the other species of sect. *Eucnide*.

Renewal growth in *E. cordata* is dichasial. Renewal branches arise in the axils of two leaves subjacent to the floral nodes. It is usually below the region where extensive internodal elongation occurred concurrent with flowering. Each renewal axis may or may not be recalescent with its subtending leaf.

Sect. SYMPETALEIA. *Eucnide aurea* and *E. rupestris* have an inflorescence pattern similar to that identified as the most common among the species of sect. *Eucnide*. Each lateral floral axis of *E. aurea* and *E. rupestris*, examined on herbarium specimens, may be monochasial (Fig. 6) or dichasial (Fig. 5) (as also was true of most species of sect. *Eucnide*). *Eucnide tenella* (Fig. 9), unlike these other species of sect. *Sympetaleia*, lacks distinct lateral floral branches and renewal branches. Axes (Fig. 9; initial axes were unavailable on herbarium specimens) produce either one or two leaves and a terminal flower. Each leaf of an axis usually is recalescent with its axillary bud. Each of these axillary buds reiterates the pattern of producing one or two leaves (each of which usually will be recalescent with its axillary bud) and a terminal flower.

Unlike the other species grown under glasshouse conditions, *E. aurea* is likely to have up to six flowers that open concurrently on a single renewal axis. In the other species, usually only one or two flowers associated with any one renewal axis were observed to be open concurrently. The internodes of the lateral floral axes of *E. aurea* also elongate to a greater extent over the period of flowering than do the corresponding internodes in most species of sect. *Eucnide*.

Renewal growth in *E. aurea* appears to be primarily monochasial (Fig. 3). As in the other species, the primary renewal axis is one of the recalescent axillary buds subjacent to the terminal flower. Other reiterative lateral shoots with a vegetative phase (i.e., producing more than two leaves before forming a terminal flower) begin growth after the renewal shoots from an axis have begun to flower. Renewal

growth of *E. rupestris* was impossible to determine from herbarium specimens.

Sect. MENTZELIOPSIS. *Eucnide urens* (Fig. 10) is distinct in having terminal flowers displaced from the notch between the two subjacent lateral flowering axes. In some of the other species, the terminal flowers of vegetative axes are sometimes somewhat confluent with the uppermost lateral axis that is flowering (concaulescence, sensu Troll 1964). The actual developmental process that causes this displacement in *E. urens* is unclear, although it also appears to be concaulescence. The lateral floral shoots in *E. urens* (Fig. 6) largely are the same as in most species of sect. *Eucnide*, except for the distinctive terminal flower displacement. *Eucnide urens* also differs from the species in sects. *Eucnide* and *Sympetaleia* because the leaf directly beneath a terminal flower is clasping. Renewal growth data for *E. urens* is unavailable because I could not obtain adequate growth of this species in glasshouse populations.

DISCUSSION

Eucnide has monotelic axes (sensu Troll 1964) because each shoot terminates in a flower. Troll (1964) suggested that the Loasaceae is among a group of families characterized by monotelic synflorescences (i.e., monotelic shoots associated with the initial and each renewal axis).

Inflorescences in *Eucnide* were first described as cymes (Urban 1886). Urban (1892) later described inflorescence patterns in various loasaceous species, including *E. bartonioides*. For *E. bartonioides*, he described two or three floral branches beneath the terminal flower. Each floral branch was observed to be adnate with its subtending leaf and to produce two prophylls before terminating in a flower. Each prophyll subtended a similar branch and was likewise adnate with it. His set of observations concur with the patterns I have described for *E. bartonioides*, and generally characterize the patterns found among most of the species (*E. cordata*, *E. tenella*, and *E. urens* are divergent the most notably).

No major distinctions in inflorescence architecture seem to differentiate sect. *Sympetaleia* from sect. *Eucnide*. Within both sections there are variations (*E. cordata* in sect. *Eucnide* and *E. tenella* in sect. *Sympetaleia*) from the commonly expressed patterns. Gilg (1925) described *Eucnide* as having flowers arranged in cymes (presumably implying dichasia in this instance) and monochasia. He described the genus *Sympetaleia* (synonymized with *Eucnide* by Thompson and Ernst, although they segregated these species into sect. *Sympetaleia*) as having flowers arranged in few-flowered cymes. Gilg's use of the term cyme appears to imply a dichasial branching pattern

in the inflorescence, and this concurs with my observations of dichasial inflorescences in *E. aurea* and *E. rupestris*. Although the initial and renewal axes tend to form two lateral floral axes (dichasia) in *E. aurea* and *E. rupestris*, I have observed that the successive iterations of floral branches from each of these lateral floral axes may be either dichasial or monochasial.

Eucnide tenella is the only species of *Eucnide* that probably should not be considered to have either a monochasial or dichasial cyme. This species was described (Johnston 1924) only a year before Gilg (1925) published descriptions of *Eucnide* and *Sympetaleia*, and *E. tenella* was not included among them. The growth pattern of *E. tenella* appears to be a simplification of that found in the other species of *Eucnide* because it has neither distinct lateral floral branches nor distinct renewal branches that produce more than two leaves before conversion to flowering. The branches in *E. tenella* are similar to the lateral floral branches of the other species because they produce only one or two leaves and then a terminal flower. They differ from these branches because they do not die back after a flush of flowering; instead, they appear to continue producing one or two leaves (each with iterative axillary buds) and a terminal flower. Thus, the inflorescence in *E. tenella* is limited to the terminal flower produced by each axis. This alteration implies that whole plant architecture in *E. tenella* would differ significantly from the other species of the genus.

Among the species of sect. *Eucnide*, *E. cordata* has the most divergent inflorescence architecture because its penultimate internodes are distinctly elongated, as are those of the lateral floral branches. Waterfall (1959) noted this distinct architectural pattern in *E. cordata* and characterized the inflorescence as "lifted above the leaves on a short peduncle." He considered this to be the greatest tendency toward a terminal inflorescence in the genus.

Eucnide aurea and *E. cordata* may invest more heavily in flowers than other species. Both have a number of flowers that approach maturity simultaneously on inflorescence systems with extensive internodal elongation. In other species, floral buds remain small and inflorescence internodes are unextended until a particular flower begins to mature. *Eucnide cordata* and *E. aurea*, along with *E. rupestris* (the development of which I have not examined), are the only species that Thompson and Ernst (1967) reported to have many, crowded flowers in their inflorescences. These three species and *E. tenella* are primarily centered in Baja California, whereas the other *Eucnide* species are distributed throughout mainland Mexico and southwestern United States. Whether these similarities among species distributed in Baja California represent common ecological adaptations, phylogenetic constraints, or merely coincidental convergences should be investigated further. I have shown previously

(Hufford 1986) that individual flowers of *E. aurea* tend to be longer-lived following anthesis than flowers of other species of *Eucnide* (the same species as grown in glasshouse populations) that were investigated for this study. The persistence of individual flowers also may make this species appear to have many flowers that mature simultaneously.

The displaced terminal flowers of *E. urens* appear to be an extreme modification of the slight concaulescence that was observed commonly among the other species. *Eucnide urens* also differs from the other species because the leaf subtending a terminal flower is clasping. Waterfall (1959) noted that the "uppermost leaves [were] sometimes sessile and slightly amplexicaul". In the other species, leaves in the inflorescence region were often quite reduced, but they remained petiolate and were never clasping. These divergent features in the inflorescence region of *E. urens* support Thompson and Ernst's (1967) segregation of this species into its own section. Cladistic analysis of *Eucnide* (Hufford 1986) has shown that the *E. urens* complex is probably a sister group to the rest of the genus. The inflorescence features are among a suite of unique characteristics possessed by *E. urens* within the genus.

When Waterfall (1959) delineated two series in *Eucnide* based on inflorescence positions (the first series had solitary flowers in leaf axils and the second series had terminal inflorescences), he noted, "collections from young plants beginning to flower might be confused with the first group" (i.e., those thought to have solitary flowers in leaf axils). This observation is likely to be true because Waterfall and Thompson and Ernst (1967) each characterized at least some of the species as possessing axillary flowers. Axillary flowers have not been present in any of the material I examined. It is likely that the analyses presented in these systematic revisions were confused by the condensed internodes in the flowering region, the extended developmental period of the lateral floral branches, and the recaulescence in the floral branches. An accurate analysis of the inflorescence pattern in *Eucnide* would have been difficult without observation of the growth patterns of living plants. It is exceptionally difficult to determine inflorescence and branching patterns from herbarium specimens. Further comparative studies of 1) the developmental origin of the recaulescence common to most or all of the species, 2) the elongated internodes associated with the inflorescence region of *E. cordata*, and 3) the displacement of terminal flowers of *E. urens* are warranted.

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A SYSTEMATIC STUDY OF *SILENE SUKSDORFII*,
S. GRAYI, AND *S. SARGENTII*
(CARYOPHYLLACEAE)

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ABSTRACT

The taxonomic and geographic limits of *Silene suksdorfii*, *S. grayi*, and *S. sargentii* are not well defined in California. Specimens of *Silene* from subalpine and alpine regions have been regarded traditionally as either *S. grayi* or *S. sargentii*. Several collections from northern California possess features characteristic of *S. suksdorfii*. Evidence from morphological, ecogeographical, and phytochemical examinations is presented that clarifies the taxonomic relationships, delimits the differences among these species, and corroborates the existence of *S. suksdorfii* in California.

Silene has been the subject of several regional and worldwide taxonomic revisions (Williams 1896, Robinson 1897, Hitchcock and Maguire 1947, Chowdhuri 1957). Although many species are circumscribed clearly, others are polymorphic or possess characters that do not permit clear distinctions to be made, and information about the distribution and habitat(s) of these species often is lacking or defined poorly. Historically, subalpine and alpine specimens of *Silene* from the southern Cascade Range of California have been considered to be either *S. grayi* Wats. or *S. sargentii* Wats. The occurrence of *S. suksdorfii* Robins. on Mount Shasta has been overlooked generally, and examination of herbarium records and pertinent literature indicates that the distributional ranges of these three species are not well understood.

Robinson (1891), Hitchcock and Maguire (1947), and Chowdhuri (1957) commented on the similar morphology of *S. suksdorfii*, *S. grayi*, and *S. sargentii*. Traits that typically distinguish *S. suksdorfii* from *S. grayi* and *S. sargentii* are its shorter stature, shorter basal leaves, bilobed petal blades, and trichomes of the calyx that possess purple septal walls. *Silene suksdorfii* is differentiated further from *S. grayi* by the presence of anastomosing calyx veins, and from *S. sargentii* by epapillose seeds.

Hybridization studies by Kruckeberg (1955, 1961) showed that *S. suksdorfii*, *S. grayi*, and *S. sargentii* are distinct species. Kruckeberg (1955) ascribed the high degree of sterility in hybrids to meiotic abnormalities during microspore formation and observed little chromosome pairing in hybrids. Kruckeberg (1961) concluded that vegetative and reproductive features showed that extensive genetic dif-

TABLE 1. POPULATION DESIGNATIONS USED IN FIGS. 1-4. * = putative populations of *Silene grayi* and/or *S. sargentii* determined to be *S. suksdorfii*.

SILENE SUKSDORFII	
BT	Broken Top, Three Sisters Wilderness Area, OR
SS	South Sister, Three Sisters Wilderness Area, OR
BU*	Bumpass Mt., Lassen Volcanic National Park, CA
CRE*	Crescent Crater, Lassen Volcanic National Park, CA
LA*	Lassen Peak, Lassen Volcanic National Park, CA
SP*	South Plug, Lassen Volcanic National Park, CA
RB*	Red Butte, Mount Shasta, CA
SILENE GRAYI	
MM	Marble Mountain, Marble Mountains Wilderness Area, CA
LMH	Little Mount Hoffman, Medicine Lake Highlands, CA
PSM	Pumice Stone Mountain, Medicine Lake Highlands, CA
PAN	Panther Creek Meadows, Mount Shasta, CA
SHA	Glacial basin north of Red Butte, Mount Shasta, CA
TAL	Talus at base of Red Butte, Mount Shasta, CA

ferentiation in these and most other western North American *Silene* species was complete. In spite of their genetic isolation, these three species have similar morphology and ecological preferences, which have contributed to the confusion in their delimitation in California. The purpose of the present study is to examine these species by the use of morphological, ecogeographical, and phytochemical analyses to circumscribe them clearly.

MATERIALS AND METHODS

Specimens of *S. suksdorfii* and *S. grayi* were collected in Oregon and California (Table 1). Extensive collections of *S. sargentii* were not made during this study because the taxon is represented amply in California herbaria.

Field collections of *S. suksdorfii* and *S. grayi* were used in chemical analyses. Flavonoid compounds were extracted from dried flowers, purified, and identified using two-dimensional paper chromatography following standard techniques (Harborne 1967, Mabry et al. 1970). The first phase was developed in 4:1:5 butanol:glacial acetic acid:water (BAW); the second, in 15% glacial acetic acid. Rutin provided a reference marker. For spectrophotometric analyses, extracts from dried flowers were streaked onto Whatman 3 mm paper and developed in four solvent systems: BAW, 15% glacial acetic acid, BEW (4:1:2.2 butanol:ethanol:water), and water. Each band in each system was examined using UV light, with and without exposure to ammonia fumes. Identification of compounds was made using UV spectroscopy. Sugar moieties were not identified during

TABLE 2. MORPHOLOGICAL CHARACTERS AND DIAGNOSTIC FEATURES OF *Silene suksdorfii*, *S. grayi*, AND *S. sargentii*. Adapted in part from Hitchcock and Maguire (1947). ¹ = definitive for species; ² = variable, but definitive in combination with other characters. All measurements are in millimeters except where noted.

	S. SUKSDORFII	S. SARGENTII	S. GRAYI
Stature ² , cm	3-10(-15)	10-15(-20)	10-20(-30)
Stem glandularity	glandular above; increases from base	glandular above	glandular above; can be eglandular below
Leaves ²	matted; linear to linear-oblancoolate	tufted, marcescent; linear-oblancoolate	tufted, thickened, \pm fleshy; linear-oblancoolate to oblancoolate-spatulate
Leaf glands	present	present	absent
Leaf length	(5-)15(-50)	15-25(-40)	(15-)20-40(-60)
Leaf width	1.5-2(-4)	(1-)1.5(-3)	(1-)2-5(-7)
Calyx length	10-14(-18)	(8-)10-14(-17)	(7-)10-12(-13)
Calyx trichomes ¹	purple-septate	hyaline-septate, rarely purple-septate	hyaline-septate
Calyx nerves ¹	anastomosing; purple	anastomosing; green-purple	nonanastomosing; green-purple
Petal claw	(7-)8-11(-13)	(8-)10-14(-17)	8-11
Petal blade	(3-)3.5(-5)	2.5-3.5(-5)	(3-)3.5(-5)
Petal lobing ²	bilobed with occasional small lateral teeth	bilobed with small lateral teeth	more or less four-lobed, rarely bilobed
Carpophore	(2-)2.5-3.5	1.5-3	(1.5-)2-3
Style number	3(4)	3(4.5)	3
Seed length ¹	1.1-2.0 (\bar{x} = 1.6)	1.2-2.0 (\bar{x} = 1.5)	1.8-3.0 (\bar{x} = 2.3)
Testa character ¹	tessellate	tessellate with marginal papillae	tessellate

this study. Flavonoids isolated from putative populations of *S. suksdorfii* were compared to those extracted from different populations of *S. grayi* and *S. suksdorfii*. Flavonoids of *S. sargentii* were not examined because this species possessed distinctive morphological traits.

Morphological measurements were made using field and herbarium specimens to corroborate those given by Hitchcock and Maguire (1947). Statistical tests included F-test, Student's t-test, and arcsin transformation methods (Sokal and Rohlf 1973). Seeds were measured using a micrometer calibrated for use with a dissecting microscope.

Specimens were examined from CAS, DS, F, GH, JEPS, MO, NY, ORE, OSC, PH, UC, US, WS, and WTU. Voucher specimens are deposited in CAS, SFSU, and WTU. Nomenclature conforms to Munz (1959) and Hitchcock et al. (1969).

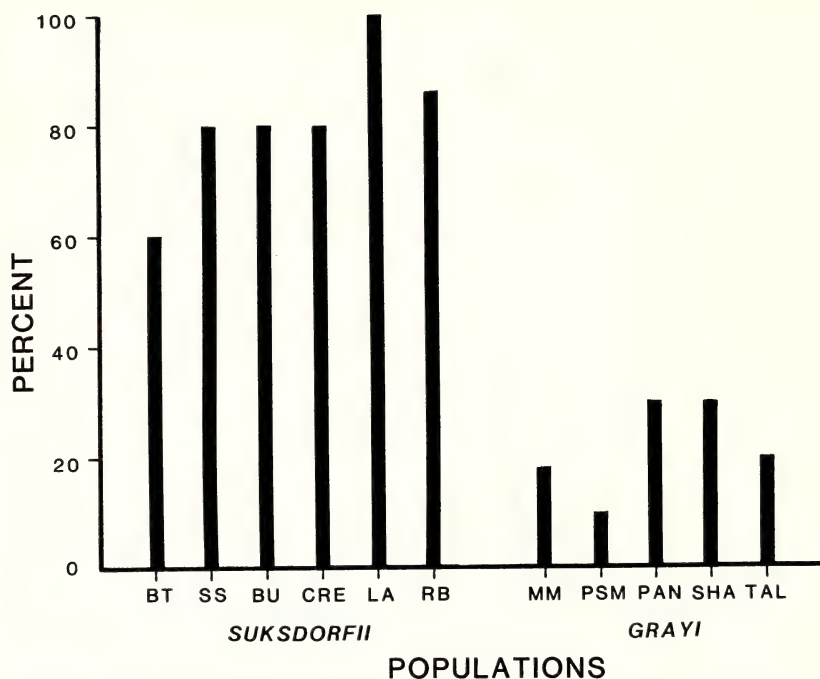


FIG. 1. Percent anastomosing calyx veins in populations of *Silene suksdorfii* and *S. grayi* (n = 40).

RESULTS

Morphology. Morphological characters were studied with specific reference to those given by Hitchcock and Maguire (1947) and are shown in Table 2. Traits that were valuable in the differentiation of *S. suksdorfii* from *S. grayi* and *S. sargentii* were the presence of purple-septate calyx trichomes, the absence of corolla lobes lateral to primary lobes, seed size, and lack of marginal papillae on seeds. *Silene grayi* and *S. sargentii* possess hyaline-septate calyx trichomes and corolla lobes lateral to primary lobes. Seeds of *S. grayi* are larger than those of *S. sargentii* or *S. suksdorfii*, and seeds of *S. sargentii* possess marginal papillae. Calyx venation is an additional feature by which *S. suksdorfii* and *S. sargentii* can be distinguished from *S. grayi*.

Robinson (1891) distinguished *S. grayi* and *S. suksdorfii* using calyx venation. He reported veins of *S. grayi* as simple and those of *S. suksdorfii* as anastomosing. An examination of specimens of *S. sargentii* also indicates that calyx veins are primarily anastomosing in this taxon. Although this trait is variable in these three species, presence or absence of anastomosing calyx veins can be a

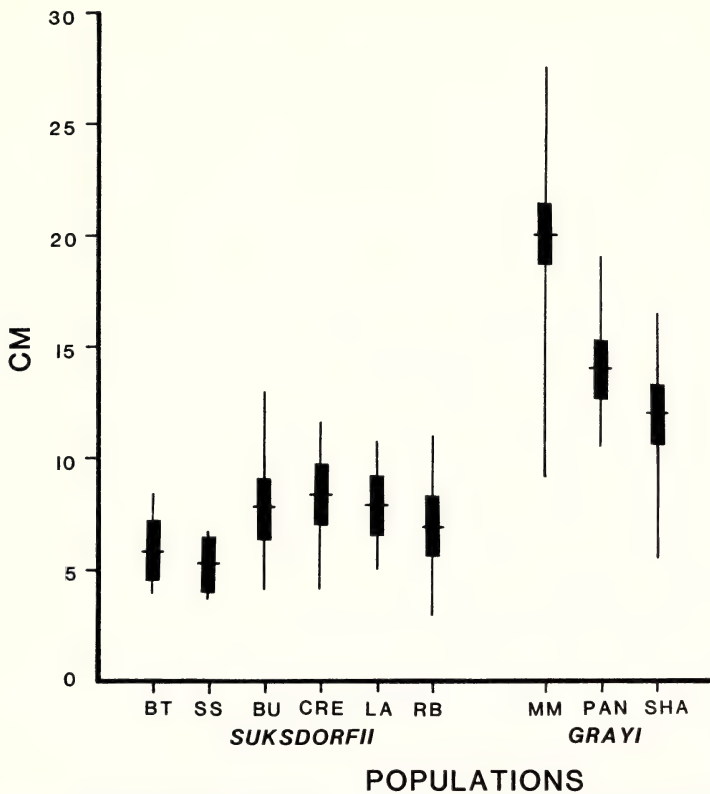


FIG. 2. Comparison of stem length in populations of *Silene suksdorfii* and *S. grayi* [$n = 15$; 1.96 ± 1.3 ($\bar{x} \pm \text{s.e.}$)].

significant feature. I found that the presence of anastomosing calyx veins in *S. suksdorfii* was significant in the differentiation of *S. suksdorfii* from *S. grayi* ($p < 0.05$). The differences between these species was greater than the natural variation within each species (Fig. 1). Anastomosing calyx veins in *S. sargentii* were not analyzed statistically due to inadequate sample sizes. Differences in calyx length/width between *S. suksdorfii* and *S. grayi* were not significant statistically ($p > 0.05$). In general, calyx size is not a reliable taxonomic trait in the differentiation of species of *Silene* because the developing capsule deforms the calyx, which renders field measurements inaccurate (Bocquet and Baehni 1961). Robinson (1891), Hitchcock and Maguire (1947) and Chowdhuri (1957) attributed shorter stature to *S. suksdorfii* than to *S. grayi* or *S. sargentii*. Leaves of *S. suksdorfii* were described similarly as being smaller than those of the other two species. In the examined populations, *S. grayi* is taller than *S. suksdorfii* ($p < 0.05$; Fig. 2). Stature in *S. sargentii* is

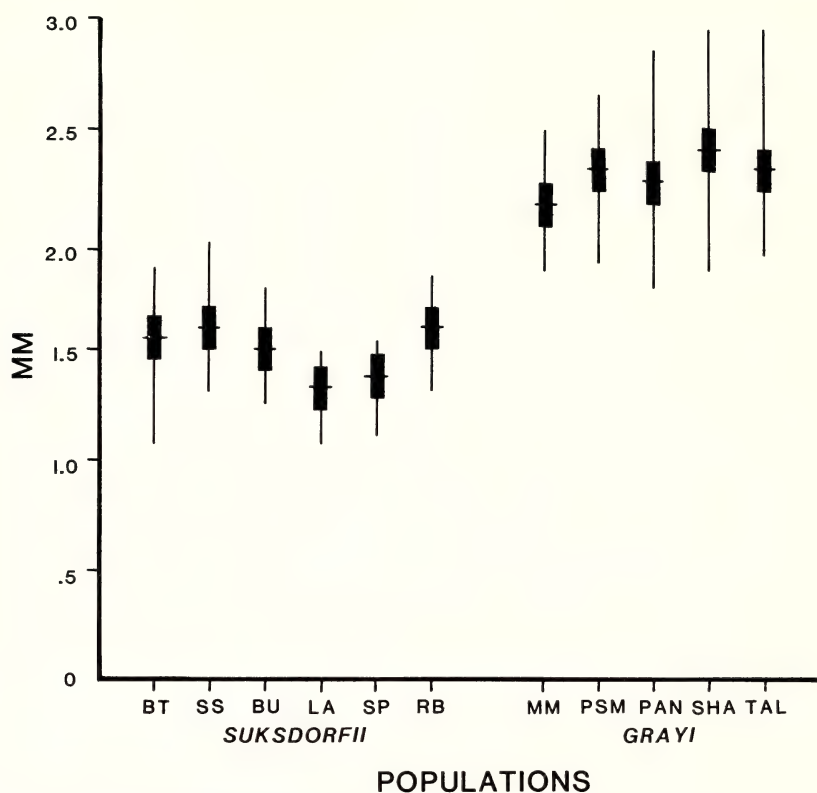


FIG. 3. Comparison of seed length in populations of *Silene suksdorfii* and *S. grayi* [$n = 20$; 1.96 ± 0.09 ($\bar{x} \pm \text{s.e.}$)].

similar to that of *S. grayi*. Differences in the size of basal leaves of *S. suksdorfii* and *S. grayi* were not significant ($p > 0.05$). The leaves of *S. suksdorfii* and *S. sargentii* appear narrower than those of *S. grayi*. Seed length in *S. suksdorfii* and *S. sargentii* was similar in range and average size. *Silene suksdorfii* had significantly different seed lengths in comparison to *S. grayi* ($p < 0.05$; Fig. 3).

Flavonoid analysis. The two-dimensional spot configuration was similar for *S. suksdorfii* and *S. grayi*, but iso-orientin, a c-glycosyl-flavonoid, was present on chromatograms of *S. grayi*.

Distribution. *Silene suksdorfii* occurs at elevations of 1800–3000 m, and is restricted to alpine environments on volcanic peaks in the Cascade Range. Prior to the present study, *S. suksdorfii* was reported solely from the major Cascade Range peaks of Oregon and Washington, and although Merriam (1899) reported correctly that *S. suksdorfii* occurred on Mount Shasta, its existence in California has been

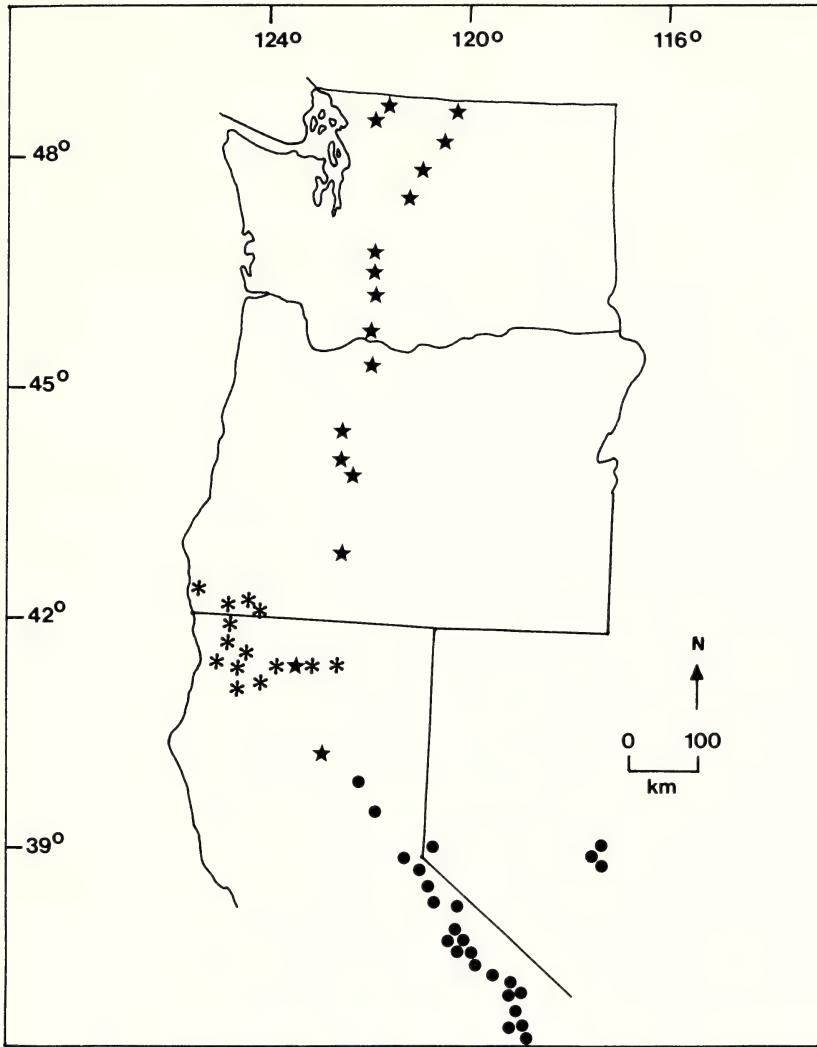


FIG. 4. Distribution of *Silene suksdorfii* (★), *S. grayi* (*), and *S. sargentii* (●). Locations are based on herbarium specimens and from literature, and represent the corrected distribution of each species.

largely overlooked. In California, *S. suksdorfii* is represented by populations on Mount Shasta (Red Butte and Lake Helen) and on several peaks within Lassen Volcanic National Park (Table 1). *Silene grayi*, found at 1200–2900 m elevations, is an element of several disparate ecosystems: montane chaparral, montane forest, subalpine forest, and alpine. Substrates on which it occurs include gabbro, granite, marble, serpentine, andesite, and rhyolite pumice. It occurs

in the Klamath Mountains Province of Oregon and California; in California, it also occurs in the Medicine Lake Highlands and on Mount Shasta, the type locality. *Silene grayi* is sympatric with *S. suksdorfii* on Mount Shasta. *Silene sargentii*, also an alpine species, occurs at elevations of 2400–3800 m, and is found primarily on granitic, metamorphic, and volcanic substrates. In California, it occurs on Sierra Nevada peaks from Inyo to Plumas cos.; in Nevada, it occurs on Mount Rose, and in the Monitor, Toiyabe, and Toquima ranges.

The distributions of *S. suksdorfii*, *S. grayi*, and *S. sargentii* reported previously in the literature are inaccurate due to misidentification of herbarium specimens. Collections reported as *S. sargentii* from the Cascade Range are either *S. suksdorfii* or *S. parryi* (Wats.) Hitch. & Maguire. Specimens identified as *S. sargentii* from the Klamath Mountains Province are collections of *S. grayi*. Similarly, individuals identified as *S. grayi* from the Cascade Range of Oregon and Washington are either *S. suksdorfii* or *S. parryi*. The report of *S. grayi* from the Webber Lake Mountains, Sierra Co., California, by Hitchcock and Maguire (1947) is based on a collection of *S. bernardina* Wats. ssp. *maguirei* Bocquet (= *S. montana* Wats.). Collectors (Gillett et al. 1961) also have reported *S. grayi* from Lassen Volcanic National Park, California, but examination of specimens from this location revealed they are collections of *S. suksdorfii*. Several collections of *S. douglasii* Hook. from the Cascade Range and from Mount Olympus have been misidentified as *S. suksdorfii*. Some collections of *S. sargentii* also have been misidentified as *S. suksdorfii*. The corrected distributional ranges for *S. suksdorfii*, *S. grayi*, and *S. sargentii* are illustrated in Fig. 4.

DISCUSSION

Morphology. There is considerable overlap of many morphological characters among *S. suksdorfii*, *S. grayi*, and *S. sargentii*, but seed size and morphology, calyx trichomes and venation, and petal lobing constitute a suite of taxonomic features useful in their differentiation.

The data presented here, in addition to the phylogenetic study of Williams (1896), offer several conclusions about the value of these morphological characters: 1) The use of external seed microsculpturing is valuable in delimiting *S. suksdorfii*, *S. grayi*, and *S. sargentii* (see Crow 1979, Prentice 1979, Wofford 1981). The prominent papillae on seeds of *S. sargentii* are diagnostic. 2) Seed length in *S. grayi* is 1.8–3.0 mm, not 1.5 mm as reported by Hitchcock and Maguire (1947). 3) The presence of purple-septate trichomes is valuable in delimiting *S. suksdorfii*. Purple-septate trichomes are not known in *S. grayi* and are rare in *S. sargentii*. The occasional oc-

currence of these trichomes in *S. sargentii* does not diminish the importance of this trait in circumscribing *S. suksdorfii*. 4) Calyx veins are primarily anastomosing in *S. suksdorfii* and *S. sargentii* and are nonanastomosing in *S. grayi*. 5) Petal blades in flowers of *S. suksdorfii* typically are bilobed and lack lateral teeth; those in *S. sargentii* usually possess small lateral teeth, and lateral lobes commonly are prominent in *S. grayi*.

Chemotaxonomy and pollination. The presence of iso-orientin in *S. grayi* floral extracts and its absence in those of *S. suksdorfii* provides additional evidence to support the present taxonomic and distributional circumscriptions of these species. Because flavonoids may function in UV absorption as nectar guides, differences in floral chemistry may result from adaptations to different pollinators (Thompson et al. 1972, Harborne 1975). In higher plants, differences in floral morphology that attract different types of pollinators to different species or reduce the possibility of cross pollination between two species are effective prezygotic isolating mechanisms (Stebbins 1977). If floral structure is similar, then diurnal or vespertine flowering also may serve as an isolating mechanism. *Silene suksdorfii* is a diurnal species, whereas *S. grayi* is vespertine. Sphingid moths (after sunset) and syrphid flies (at dawn) were observed visiting *S. grayi*. No pollinators have been observed on *S. suksdorfii*.

Ecology. Detailed ecological information is not widely available for *S. suksdorfii*, *S. grayi*, or *S. sargentii*. Excerpts from phytosociological studies (Whittaker 1960, Pemble 1970, Hamann 1972, Taylor 1976, Burke 1982), herbarium collections, regional floras (Ireland 1968, Hunter and Johnson 1983), and field observations, however, provide insight into the types of habitats in which they occur. *Silene suksdorfii* and *S. sargentii* are found typically on well-drained substrates in similar habitats in the alpine: in soil pockets on talus slopes, in soil around boulders, and on open, windswept ridges and plateaus. Density and duration of snowpack is variable in areas in which *S. suksdorfii* is found. Populations on vertical cliff faces, such as those on Red Butte and Broken Top, are subject to winter desiccation and exposure to extreme cold. The ability of *S. suksdorfii* to grow on cliff faces may depend on the snowmelt water from snowbeds in crevices of rocks and on the ability of poikilohydric mosses to rapidly absorb snowmelt and rainfall, as well as to trap soil (Billings and Mooney 1968, Grime 1979, Walter 1979; D. W. Showers, pers. comm.). Areas in which *S. sargentii* occurs often are not free of snow until midsummer and dry out rapidly following snowmelt. Populations of *S. grayi* occur largely on well-drained substrates, but several alpine populations occur in moist, poorly-drained soils located commonly in glacial basins (e.g., Mount Shasta), or on slopes below snowfields. For example, Ferlatte (1974)

reported a population of *S. grayi* growing on a granitic slope below a permanent snowfield on Thompson Peak in the Trinity Alps. The presence of other moisture-tolerant taxa at this site is indicative of the poorly-drained nature of the soil.

Certain populations of *S. suksdorfii*, *S. grayi*, and *S. sargentii* occur in alpine habitats below climatic timberline. These populations occur in areas where localized climatic and edaphic conditions result in the formation of alpine-like microhabitats at elevations lower than typical of alpine habitats (Daubenmire 1954, Tranquillini 1979, Walter 1979). The existence of azonal alpine is significant in understanding the distribution of *S. suksdorfii* in California because climatic timberline in northern California occurs at 2800 m. The presence of suitable azonal alpine environments at Lassen Volcanic National Park and on Mount Shasta explains the occurrence of *S. suksdorfii* and other species typical of the alpine below that elevation.

KEY TO SPECIES

Blades of petals 2-lobed or with 4 unequal lobes.

Calyx 8–10 mm long; calyx trichomes hyaline-septate; blades of petals 3–5 mm long; basal lvs. 2–5 mm broad; seeds tessellate, ca. 2–3 mm long. n. CA and s. OR *S. grayi*

Calyx 10–14 mm long; blades of petals 2.5–3.5 mm long; basal lvs. 1–2 mm broad; seeds ca. 1.5 mm long.

Calyx trichomes hyaline-septate (rarely purple-septate); seeds with tessellate faces and marginal papillae (visible with hand lens). Plumas to Inyo cos., CA; NV . *S. sargentii*

Calyx trichomes purple-septate; seeds tessellate, without marginal papillae. Volcanic peaks, Shasta and Siskiyou cos., CA; n. *S. suksdorfii*

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ANNOUNCEMENT

MARY DeDECKER SYMPOSIUM

Co-sponsored by the
University of California White Mountain Research Station
The California Native Plant Society
The Bristlecone Chapter of the CNPS
30 April, 1-3 May 1987
Bishop, California

The University of California White Mountain Research Station with the California Native Plant Society and its Bristlecone Chapter are co-sponsoring a symposium and field trip honoring Mary DeDecker. The topic of the symposium is the flora and plant biology of the eastern Sierra, Owens Valley, White-Inyo Mountains and western Basin and Range Provinces. Palynology and legislation related to preservation of plants in eastern California and western Nevada also are included as symposium topics.

A field trip will be lead by Mary DeDecker, a member of the BLM staff, and others to the Eureka Dunes on Saturday, 2 May. A cookout-BBQ will be held in the Eureka Dunes following the field trip.

For additional information contact Dr. Clarence A. Hall, Jr., White Mountain Research Station, 6713 Geology Building, University of California, Los Angeles, CA 90024; phone: (213) 825-2093.

CLARKIA CONCINNA SUBSP. *AUTOMIXA* (ONAGRACEAE),
A NEW SUBSPECIES FROM THE SOUTH BAY
REGION, CENTRAL CALIFORNIA

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ABSTRACT

Clarkia concinna subsp. *automixa* Bowman is described from the South Bay Region of central California. Unlike typical *C. concinna*, this subspecies is not protandrous and is highly modified for selfing.

Clarkia concinna (Fischer & Meyer) Greene was described in 1835 from material collected near Fort Ross, Sonoma Co., California. Despite generic revision (Greene 1891), the species has remained intact, based on its distinctive petal configuration and possession of four anthers, a condition unique within sect. *Eucharidium*. The section contains two species, *C. concinna* and *C. breweri* (Gray) Greene (Lewis and Lewis 1955); both are endemic to northern and central California. Investigations of breeding systems within sect. *Eucharidium* have revealed two dissimilar forms within *C. concinna*. The southern form is strongly, if not exclusively, selfing. Further field investigations and examination of herbarium material support the taxonomic distinctness of this group, which I propose herein as a new subspecies.

Clarkia concinna (Fischer & Meyer) Greene subsp. *automixa* Bowman
subsp. nov.

Subspecies *fabricata*, *antheris distinctis*. Flores *nonproterandri*, *automixi*, *claudentes noctu*; *petala* 12 mm *longa*. *Chromosomata* *numero* $2n = 14$ (Figs. 1–5).

Annual, erect to diffusely branched, to 4 dm tall; stems glabrate or with minute, upwardly curled hairs. Leaves elliptic to ovate, entire, 2–3(–4.5) cm long, 6–20 mm broad, narrowed to petioles 5–25 mm long. Rachis of the inflorescence erect. Flowers erect in bud, becoming deflexed; sepals linear or narrowly oblanceolate, 1–2 cm long, 1–2 mm wide, commonly remaining united at the tips at anthesis, sharply deflexed at the middle, deep red and petaloid at the base; petals deep bright pink, the claw not streaked with white or purple, 8–12(–17) mm long, 4–8 mm broad, the blade 3-lobed, the lobes shallow, (2–)3–4 mm deep, petals closing the flower at night;



stamens 4, roughly equal, surrounding the style, filaments pinkish-lavender; anthers without hairs or only slightly ciliate, curling after dehiscence; pollen bluish with copious viscin threads; stigma white, obscurely 4-lobed, appearing capitate or bifid at maturity, receptive prior to or at anthesis, positioned with the anthers, clearly not protandrous. Chromosome number $2n = 14$. Flowering from mid-May to late June.

TYPE: USA, California, Santa Clara Co.: Mt. Hamilton Range, along Kincaid Rd., 11.1 km n. of Smith Creek Ranger Station, w.-facing slope 3 m e. of road in grassy oak woodland and ca. 300 m s. of locked gate across road, R3E T6S S29 nw.¼ nw.¼ (Mt. Day quad.), 37°23'13"N, 121°39'26"W, elev. 735 m, 29 May 1986, *Bowman 7001* (Holotype: UC; isotypes: CAS, CS, CSUC, GH, LA, MO, RSA, SJSU).

PARATYPES: USA, California, Alameda Co.: 2.4 mi w. of Sunol, 14 May 1938, *Constance 2233* (CAS, GH, RSA, UC). Santa Clara Co.: Montebello Rd., 3.1 mi w. of Stevens Canyon Rd., 16 Jun 1983, *Bowman 3202* (CS, CSUC, UC); 11.3 mi s. of Alum Rock Ave. on Mt. Hamilton Rd., 16 May 1985, *Bowman 6035* (CS, CSUC, UC); jct. Stevens Canyon Rd. and Redwood Gulch Rd., 24 May 1985, *Bowman 6076* (CS, CSUC, UC); Soda Spring Canyon, 28 May 1895, *Dudley 4029* (RSA); Congress Springs, 13 May 1904, *Heller 7412* (DS, GH, UC); Booker School near Saratoga, 19 May 1906, *Pendleton 346* (POM, UC); Poverty Flat, Henry Coe St. Park, 10 May 1972, *Powers 581* (SJSU); Smith Creek, 7 May 1934, *Sharsmith 1016* (DS, RSA, UC); headwaters of Stevens Creek, 3 Jun 1961, *Thomas 9517* (DS, RSA).

Distribution. *Clarkia concinna* subsp. *automixa* is limited to Santa Clara and southern Alameda cos., California (Fig. 6). Although it occurs extensively in the foothills surrounding the Santa Clara Valley, this subspecies is known only from Sunol Canyon in Alameda Co. It is common in mesic, shaded oak woodlands. In contrast, subsp. *concinna* ranges from extreme northwestern California southward to the Oakland Hills (Alameda Co.) and Mt. Diablo (Contra Costa Co.). The two subspecies are allopatric and are separated by a minimum distance of ca. 33 km.

←

FIGS. 1–5. Floral variation in subspecies of *Clarkia concinna*. Specimens grown from field collections as indicated. 1. Top row, subsp. *concinna*, l. to r., *Bowman 6070*, *3336*, *6074*; bottom row, subsp. *automixa*, *Bowman 3685*, *3687*, *3302*; all at 1×. 2. Stigma exertion in subsp. *concinna*, *Bowman 6073*; 2×. 3. Stages in the protandrous development of subsp. *concinna* flowers. The interval between anthesis (top) and stigmatic receptivity (bottom) is 1–2 days; ca. 2×. 4, 5. Self-pollination in subsp. *automixa*, *Bowman 6036*; 2×. Stigmas in subsp. *automixa* are not protandrous and are positioned with the anthers at dehiscence.

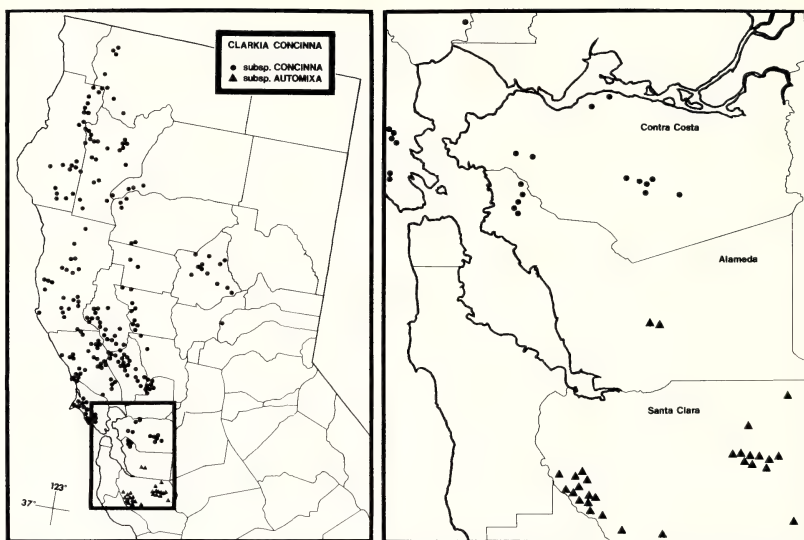


FIG. 6. Geographical distribution of *Clarkia concinna* subsp. *concinna* and subsp. *automixa* in northern and central California.

Morphology and pollination. *Clarkia concinna* subsp. *automixa* is distinguished by a combination of characters that promote selfing. Its flowers are smaller and markedly less variable (Fig. 1) than those of subsp. *concinna*, which are predominately outcrossed. Throughout its entire range, subsp. *concinna* is strongly protandrous (Figs. 2, 3); its anthers and stigmas are isolated temporally and spacially. The flowers of subsp. *automixa* are not at all protandrous (Figs. 4, 5) because the stigma becomes pollen-receptive before the bud opens and anther dehiscence occurs as the flower opens. The stigma is positioned in close proximity to the anthers, thus, facilitating self pollination. The corolla of subsp. *automixa* also lacks white streaks, particularly along the base of the claw, which are characteristic of subsp. *concinna*. MacSwain et al. (1973) noted that flowers in *C. concinna* remain open at night, an observation correct for all known populations of subsp. *concinna*. In contrast, all populations of subsp. *automixa* possess corollas that close tightly at night and appress anthers against the stigma, thus, promoting selfing. Undisturbed greenhouse plants of subsp. *concinna* generally fail to set seed, whereas those of subsp. *automixa* routinely set full complements of seeds. This confirms that the combination of morphological characters unique to subsp. *automixa* serves to facilitate selfing.

Figure 7 depicts the distribution of stamen/style ratios measured from all specimens of *Clarkia concinna* available at CAS, CS, CSUC, DS, GH, HSC, JEPS, POM, RSA, SACT, SJSU and UC. The dis-

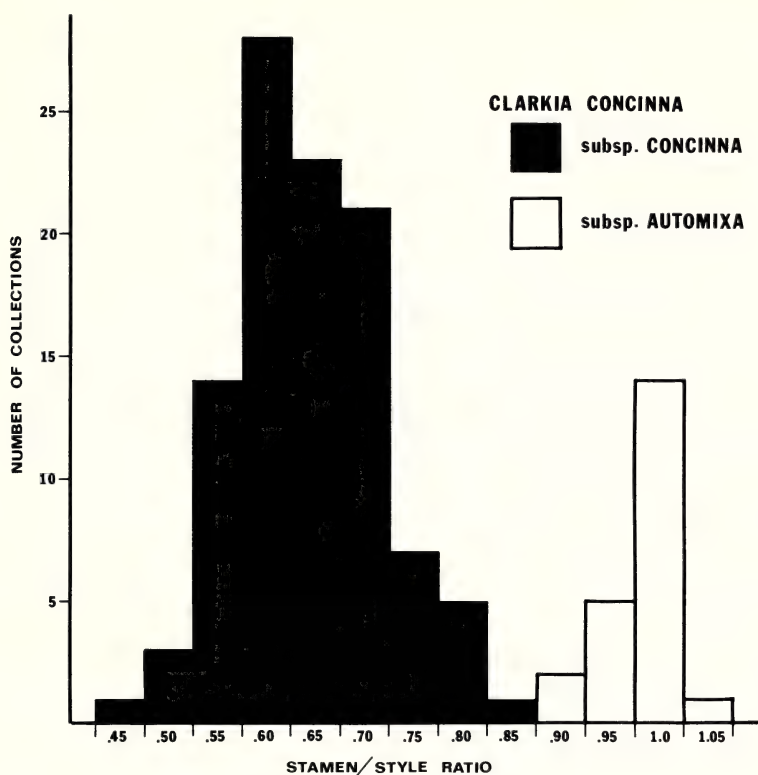


FIG. 7. Distribution of stamen/style ratios in *Clarkia concinna*. Stamens were measured from the base of the filament to the tip of the anther. Styles were measured from the distal tip of the ovary to the stigma surface. Only collections with three or more mature flowers were measured; values reported are averages of ratios from all available flowers on a specimen. Although the number of collections is clearly dependent on the total number of specimens examined, the two subspecies are defined by discontinuous stamen/style ratios.

continuous displacement of stamen/style ratios between the two subspecies agrees with evidence discussed previously. Curiously, those specimens of subsp. *concinna* (stamen/style ratio of 0.80–0.85) that most closely approach subsp. *automixa* are not from sympatric areas between the subspecies, but rather, from the extreme northern limits of the range of subsp. *concinna*. Thus, selfing may occur at both the extreme northern and southern limits of the species with allogamy predominating elsewhere. A similar pattern with selfing predominating at the margins of a species' range has been reported in *Lycopersicon pimpinellifolium* (Solanaceae) by Rick et al. (1977). Unlike the well developed autogamy in subsp. *automixa*, the northern populations of subsp. *concinna* show no signs of morphological

modification promoting selfing, other than stamen/style ratios approaching unity.

Taxonomic recognition of subsp. *automixa* is justified by comparison with other treatments in the genus. At least five *Clarkia* species have been described principally on their status as derived, primarily selfing, neospecies (Vasek and Harding 1976, Lewis 1973). Several subspecies in the genus, such as *C. tembloriensis* Vasek subsp. *calientensis* (Vasek) Holsinger (Holsinger 1985), *C. gracilis* (Piper) Nelson and Macbride subsp. *gracilis*, and *C. purpurea* (Curtis) Nelson and Macbride subsp. *quadrivulnera* (Douglas) Lewis and Lewis (in Lewis and Lewis 1955), also are based predominately on their selfing habit, even though the subspecies are not isolated from their conspecifics by geographic or other strong reproductive barriers. Subspecific taxa in *C. concinna* are differentiated by absolute geographical barriers and an assemblage of morphological characters. Although possible, gene flow between the two subspecies, as demonstrated by morphological continuity, is not in evidence. Gene flow is not likely, furthermore, because pollination of subsp. *concinna* is dependent on Lepidoptera and long-tongued Diptera (MacSwain et al. 1973). These insects are not known for long distance dispersal.

Sectional affinity. The geographical range of subsp. *automixa* is perhaps not based simply on ecological preference. Its range nearly matches the northern range of *C. breweri*, the only other species in sect. *Eucharidium*. Both species occur sympatrically at Congress Springs, Loma Prieta, Mt. Hamilton, and Cedar Mountain. Even though *C. concinna* and *C. breweri* overlap geographically, strong autogamy in subsp. *automixa* within this region prevents gene flow. Otherwise, all taxa within sect. *Eucharidium* (all $2n = 14$) are easily hybridized by artificial means and the progeny are morphologically intermediate. The identical base numbers and the comparative ease with which artificial hybrids can be produced suggest that chromosomal repatterning may not have been important in evolution of the section, although it is prevalent elsewhere in the genus (Lewis 1962). Regardless of the mechanisms that enforce reproductive isolation in the section, lack of hybrids among herbarium specimens or in extensive field reconnaissance indicates that the integrity of each taxon is conserved. The factors governing evolution and reproductive isolation in the section remain to be elucidated.

ACKNOWLEDGMENTS

I thank curators of the herbaria herein cited for access to their specimens. Appreciation also is extended to R. Gardner, L. Main, and B. O'Brien for field locality information.

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ANNOUNCEMENT

NEW PUBLICATION

Flora of the Great Plains

BARKLEY, T. M. (ed.), R. E. BROOKS, E. K. SCHOFIELD (assoc. eds.), R. L. MCGREGOR (coordinator), and 11 other members of the Great Plains Flora Association (W. T. Barker, M. Bolick, S. P. Churchill, R. L. Hartman, R. B. Kaul, O. A. Kolstad, G. E. Larson, D. M. Sutherland, T. Van Bruggen, R. R. Weedon, D. H. Wilken), *Flora of the Great Plains*, Univ. Kansas Press, 329 Carruth St., Lawrence 66045, 1986, vii, 1392 pp., illus., ISBN 0-7006-0295-X, \$55.00 (hardbound). [Covers Kansas, Nebraska, North and South Dakota, e. Montana, e. Wyoming, e. Colorado, ne. New Mexico, the Texas panhandle, nw. Oklahoma, w. Missouri, w. Iowa, w. Minnesota.]

NEW RECORDS OF MYXOMYCETES FROM CALIFORNIA. VI.

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ABSTRACT

Twenty-two additional species of Myxomycetes are reported from California. Nine of these, *Comatriza ellae*, *C. longipila*, *C. penicillata*, *Didymium bahiense*, *D. verrucosporum*, *Licea lucens*, *Macbrideola argentea*, *Paradiacheopsis cribrata* and *P. microcarpa*, appear to be new records for the United States.

In the last paper of this series (Kowalski 1973), I reported that 231 species of slime molds had been reported from California. Since then, an additional 32 species have been listed from the state. These additional records resulted mainly from the work of Whitney (1980, 1982) on corticolous species and Cox (1981) on coprophilous taxa. In the present paper, 22 new records are discussed, bringing the number of species of Myxomycetes reported from California to 285.

All collections listed have been deposited in the Herbarium of the University of California (UC). The nomenclature generally follows that of Martin and Alexopoulos (1969) and, unless otherwise stated, the collection numbers are my own.

LICEACEAE

LICEA LUCENS Nannenga-Bremekamp. — Butte Co.: Chico, Upper Bidwell Park, on Live Oak bark, 24 Jan 1977, *Whitney 368*; Lower Bidwell Park, on bark of *Quercus lobata* Neé, 23 Feb 1977, *Whitney 401*. Both collections were obtained from bark placed in moist chambers to allow the fructifications to develop. The minute (ca. 50 μm in diameter) stalked, bright orange sporangia, containing strongly warted spores, are the hallmarks of this distinctive species. In her original description, Nannenga-Bremekamp (1981) states the spores are 8–10 μm in diameter; in the California collections, however, they are usually 10–11 μm in diameter.

Because of its small size, *L. lucens* appears most similar to *L. perexigua* Brooks & Keller. Both taxa have brightly shining, often stalked sporangia that are less than 100 μm in diameter. The major differences between the species are as follows: in *L. perexigua* the sporangia are yellow to dark bluish gray and the spores smooth, whereas in *L. lucens* the sporangia are orange and the spores are distinctly warted. *Licea lucens* was described originally from France,

and the present report marks only its second known occurrence. As more workers cultivate bark in damp chambers for slime molds, I predict this species will be found in many localities.

LICEA OPERCULATA (Wingate) Martin.—Alameda Co.: Oakland, Redwood Park, on bark, 4 Feb 1970, *Duran*; Berkeley, Strawberry Canyon, on bark, 29 Jan 1972, *Duran*. As with *Licea lucens*, both collections were obtained by the moist chamber technique. The stalked, urniform, operculate sporangia separate this taxon from all other members of the genus. Martin and Alexopoulos (1969) give the height of the fructifications as 0.4–1.0 mm and state that the spores are colorless by transmitted light. In the California material, the total height of the fruiting bodies reaches 1.2 mm and the spores are pale yellow by transmitted light. *Licea operculata* has been reported from numerous locations around the world and appears to be common on the bark of living trees.

RETICULARIACEAE

LYCOGALA EXIGUUM Morgan.—Butte Co.: Covered Bridge, Honeyrun Road, on decayed wood, 15 Apr 1967, 5974. This collection of the pseudocapillitium are approximately 5 μ m in diameter and the spores are small, averaging 4.5–5.0 μ m in diameter, and smooth to weakly reticulate. This taxon has been reported from many localities beyond California, but in all cases it appears to be uncommon.

ENTERIDIUM MINUTUM Sturgis.—Plumas Co.: Humbug Summit, 6700 ft., on decayed wood, 4 Jun 1966, 3320; Siskiyou Co.: Mt. Shasta, Panther Meadows Campground, 7600 ft., on decayed wood, 6 Jul 1965, 1821, 1878. Confusion as to the exact status of this species has existed in the past. Both Lister (1925) and Hagedorn (1944) reluctantly accepted the taxon as valid, whereas Martin and Alexopoulos (1969) thought it was a small form of *Enteridium olivaceum* Ehrenberg [*Reticularia olivacea* (Ehrenb.) Fries]. The problem originated because all workers stressed the size of the fructifications. Lister thought *E. minutum* had aethalia 1–2 mm in diameter, whereas those of *E. olivaceum* were usually over 1 cm. Martin and Alexopoulos, however, thought the size overlapped and, thus, did not believe that *E. minutum* was worthy of recognition. I agree with Martin and Alexopoulos that the size of the fructifications overlap. If one looks at the spores, however, the two taxa can be distinguished easily. In *E. olivaceum*, the spores are olivaceous, occur in large clusters, usually 6–20 in number, and the ornamentation consists of large warts covering about one-half of the surface of the spores. In *E. minutum*, the spores are yellow, the clusters are small, usually consisting of 2–4 spores, and the ornamentation is minutely spinulose or warted, covering most of the surface of the spores. *Enteri-*

dium minutum is an extremely rare species. Previously it had been known only from the type locality at Eldora Lake, Colorado, and from Yorkshire, England.

CRIBRARIACEAE

CRIBRARIA FERRUGINEA Meylan. — Mendocino Co.: Simpson Lane, 2 mi e. of State Hwy 1, on decayed wood, 15 Apr 1976, 13467. The large, brick-red sporangia, 1.0–1.5 mm in diameter, with their peridial nets lacking distinct nodes and calyculi, delimits this distinct, apparently rare species. Martin and Alexopoulos (1969) give its distribution as Switzerland, Tennessee, Oregon, and New Mexico.

TRICHIACEAE

ARCYRIA MAGNA Rex. — Butte Co.: Chico, Lower Bidwell Park, on decayed wood, 4 Feb 1967, 5225; Humboldt Co.: Humboldt Redwoods State Park, on decayed wood, 26 Jan 1966, 2412. The numerous, densely clustered, grayish sporangia, which often attain a length of more than a centimeter after becoming fully expanded, separate this species from other members of the genus. Although occurring worldwide, *A. magna* is found infrequently.

TRICHIA MACBRIDEI M. E. Peck. — Butte Co.: Philbrook Reservoir, 5500 ft., on dead bark, 13 Jul 1966, 3809. This taxon can be differentiated by the dark, sessile sporangia that contain brownish spores 11–13 μm in diameter. *Trichia brunnea* Cox is the only other species in the genus that has brown spores, but it has stipitate sporangia and the spores are 10–11 μm in diameter. An unusual feature of the California collection is the capillitial threads that often terminate in depressed expansions, which resemble minute suction cups, a characteristic that has not been reported previously. *Trichia macbridei* is rare and it apparently has been reported previously only from Oregon.

TRICHIA SUBFUSCA Rex. — Humboldt Co.: Patrick's Point State Park, on decayed wood, 29 Mar 1969, 9910, and on decayed bark, 1 Apr 1969, 9967; Mendocino Co.: MacKerricher Beach State Park, on decayed wood, 12 Apr 1968, 8258. *Trichia subfusca* often has been included in *Trichia botrytis* (G. F. Gmel.) Pers., which may explain why this relatively common species has not been reported from California. The best features to use in distinguishing the two taxa are the capillitium and spores. In *T. botrytis*, the individual elaters taper gradually to long, slender, pointed tips, and the spores are 9–11 μm in diameter. In *T. subfusca*, the elaters end abruptly, often in curved, pointed tips, and the spores are (11–)12–14(–15) μm in diameter. The hypothallus in *T. subfusca* is huge, often uniting the individual sporangia into a unit, whereas in *T. botrytis* it is usually much smaller and much less extensive, rarely uniting the sporangia.

STEMONITACEAE

AMAUROCHAETE COMATA G. Lister & Brândză.—Butte Co.: Chico, Lower Bidwell Park, on dead bark, 23 Nov 1966, 3956, and 12 Feb 1969, 9899; 14 mi n. of Chico, Pine Creek Ranch, 1 Feb 1973, 12587. *Amaurochaete comata* is the only species in the genus with a capillitium consisting of flaccid, circinate threads, approximately 1–2 μ m in diameter; therefore, it is distinct. The collections cited above differ somewhat from the description given in Martin and Alexopoulos (1969). They give the diameter of the aethalia as 5–10 mm and describe the spores as prominently warted. In the California material, the aethalia are up to 5 cm in diameter and the spores are distinctly spinose. These differences may indicate that the California collections represent a different taxon. At this time, however, I do not believe that these differences are large enough to warrant the description of a new taxon. *Amaurochaete comata* was described originally from Romania. Eliasson (1977) reported it from France and Sweden and Farr (1982) reported it from Alaska. Thus, although *A. comata* seems to be rare, it has a wide distributional pattern.

COLLODERMA OCULATUM (Lipert) G. Lister.—Mendocino Co.: MacKerricher Beach State Park, on rotting wood covered with leafy liverworts, 31 Mar 1972, 12318, 12322, and 23 Mar 1972, 12316. In each of these collections, the substrate was originally collected because it had another, larger myxomycete on it. The small sporangia of *C. oculatum* were discovered later in the laboratory while the substrate was being scanned with a stereoscopic microscope. The outer gelatinous layer, unique to the genus, is scantily developed in these collections. Additionally, the spores are warted rather than echinulate as given in Martin and Alexopoulos (1969). *Colloderma oculatum* is a poorly known species; until more material is available for study, I believe it is best to take a conservative taxonomic approach and to enlarge the species concept to include the California collections. *Colloderma oculatum* is known only from a few collections in the United States. This is due undoubtedly to its small size and to it growing among bryophytes on dead wood, hidden from view. When investigators study lignicolous bryophytes thoroughly for slime molds, I predict that *C. oculatum* will be found more commonly than heretofore thought.

MACBRIDEOLA ARGENTEA Nannenga-Bremekamp & Yamamoto.—Butte Co.: 2 mi ne. of Magalia, on bark of *Cupressus macnabiana* A. Murray in moist chambers, 28 Oct 1978, *Whitney* 997, 1006, 1012 and 7 Mar 1979, *Whitney* 1062; Deer Creek Canyon, 7.5 mi w. of Ponderosa Way, on bark of *Vitis californica* Benthham in moist chamber, 4 Apr 1977, *Whitney* 418; Los Angeles Co.: Santa Catalina Island, Avalon, on bark of *Cypressus* sp. in moist chamber, 2 Sep 1978, *Whitney* 963. Within the genus, *M. argentea* can be

distinguished by its persistent peridium, long stalks that are three-fourths to four-fifths the total height, and spores having clusters of larger and darker warts. As Nannenga-Bremekamp and Yamamoto (1983) have indicated, this species probably is most closely related to *Lamproderma biaspersporum* Kowalski. Both species have hollow stipes, persistent peridia, and spores with warts of two sizes. They can be differentiated most easily on the bases of the capillitium and sporangial size. In *M. argentea*, the sporangia are approximately 0.1 mm in diameter and the capillitium is reduced, consisting of two or three branches of the columella that also branch 3–5 times and infrequently anastomose to form a weak but dark brown net. In *L. biaspersporum*, the sporangia are 0.25–0.5 mm in diameter and the capillitium is more highly developed, being formed from numerous branches of the columella, which radiate and branch many times in all directions. These branches also anastomose infrequently to form a weak, but decidedly whitish, net. Previously, *M. argentea* had been known only from moist chamber developments made from several locations in Japan. It may have been collected in the past, however, and incorrectly identified as *L. biaspersporum*. Hence, it could be much more common than previously thought.

MACBRIDEOLA MARTINII (Alexopoulos & Beneke) Alexop. — Lassen Co.: Eagle Lake Field Station, developed on bark of *Juniperus occidentalis* Hooker in a damp chamber, 23 May 1977, *Whitney 426*. This collection was assigned to *M. martinii* because it is the only species in the genus with a completely evanescent peridium and spores with clusters of larger and darker warts. Whitney's collection, however, may represent an undescribed taxon because it differs in several respects from the published descriptions of *M. martinii*. In typical *M. martinii*, the stipes are long, usually 5–10 times the diameter of the sporangia, the columella is tapering, the capillitium is smooth, and the spores are 6.5–8.0 μm in diameter. In Whitney's material, however, the stipes are only 2–4 times the diameter of the sporangia, the columella is broad and scarcely tapering, the capillitium bears conspicuous bead-like outgrowths, and the spores are much larger, 10.5–12.0 μm in diameter. Because typical *M. martinii* has been found apparently only in Jamaica, Dominica, Gambia, and Kentucky, and it is rare, I believe it prudent to consider Whitney's material an extreme variant of *M. martinii* and to wait for additional material to become available before reaching a final conclusion as to the disposition of the California form.

COMATRICHA ELLAE Härkönen. — Butte Co.: 5 mi e. of Stirling City, 4000 ft., on decayed wood, 19 Aug 1965, *2006*; Chico, Lower Bidwell Park, on decayed wood, 18 Nov 1966, *3907*; Lassen Co.: Eagle Lake Field Station, on bark of *Juniperus occidentalis* in a moist chamber, 20 Jun 1977, *Whitney 511*; Los Angeles Co.: Santa Catalina Island, Avalon, on bark of *Cupressus* sp. in a moist chamber,

2 Sep 1978, *Whitney* 962. The major features of this taxon are the small size (less than 1.0 mm in total height), globose sporangia, capillitium that forms a distinct surface net with few free ends, and the relatively long stipes that are 3–4 times the diameter of the sporangia. The California material is typical in all respects. When originally described by Härkönen (1977, as *C. nannengae*), *C. ellae* was known only from Norway and Finland. It has been reported since from Spain (Nannenga-Bremekamp and Lado 1985) and probably will be discovered wherever bark of living trees is cultured.

COMATRICHA LONGIPILA Nannenga-Bremekamp.—Sutter Co.: Sutter Buttes, on bark of living *Quercus* sp., 29 Jan 1969, 9841. This collection was made in the field, not in a moist chamber. *Comatricha longipila* appears to be most closely related to *C. laxa* Rost. Both taxa are relatively common on the bark of living trees and have sporangia that are globose to elongate in shape. Additionally, the main branches of the capillitium arise at right angles to the columella, and a distinct surface net is lacking. There are two major differences between these species: in *C. laxa*, the spores are 7–11 μm in diameter and the capillitium terminates in numerous short, free ends; in *C. longipila*, the spores are 6–7 μm in diameter and the capillitium has long free ends at the periphery. Although reported from several localities in Europe, this report appears to be the first record for North America.

COMATRICHA PENICILLATA Nannenga-Bremekamp & Yamamoto.—Nevada Co.: Donner Summit, 7200 ft., on dead wood, 24 Jun 1971, 11537. The distinctive characteristics of this species include jet-black, globose sporangia that are less than 0.2 mm in diameter with unbranched, or sparsely branched, capillitial threads ending in slight expansions. As Nannenga-Bremekamp and Yamamoto (1983) indicate, it is similar to *Paradiacheopsis fimbriata* (G. Lister) Hertel, and the two species can be differentiated as follows: in *P. fimbriata*, the columella is stout and not tapering, the capillitium radiates in all directions, and the spores are 10–14 μm in diameter; in *C. penicillata*, the columella tapers, the capillitium is brush-like, and the spores are 7.0–9.0 μm in diameter. In the original description, the height of the sporangia is listed as 0.8–1.0 mm and the spores are given as 7.0–8.5 μm in diameter. The California collection differs from the type collection, which was made in Japan (apparently the only other known collection), by having sporangia up to 2.0 mm in height and spores 8–9 μm in diameter.

PARADIACHEOPSIS CRIBRATA Nannenga-Bremekamp.—Sonoma Co.: 3 mi ne. of Asti, Thompson Property, on bark of *Quercus* sp. in moist chamber, 22 Jul 1978, *Whitney* 930; 25 Nov 1978, *Whitney* 1022. Both *P. cribrata* and *P. acanthodes* (Alexopoulos) Nannenga-Bremekamp have small sporangia, 0.6 mm or less in total height, and strongly spinose spores, 12–14 μm in diameter. In *P. cribrata*,

the capillitial threads are numerous, stout, and anastomosed at the surface so that a rigid network is formed. In *P. acanthodes*, the capillitial threads are fewer in number, finely pointed, and do not fuse to form a peripheral net. This appears to be the first report of *P. cribrata* from the Western Hemisphere.

PARADIACHEOPSIS MICROCARPA (Meylan) Mitchell.—Butte Co.: 2 mi ne. of Magalia, developed on bark of *Cupressus macnabiana* in moist chamber, 28 Oct 1978, *Whitney 1019*; Lassen Co.: Eagle Lake, 2 mi s. of Little Troxel Point, developed on bark of *Juniperus occidentalis* in moist chamber, 18 Jul 1977, *Whitney 699*. The major features of this taxon are the small sporangia, less than 1.0 mm in total height, the primary branches of the capillitium that arise at right angles to the columella and end in fine threads bearing short, spine-like processes, and the spinulose or minutely warted spores, 11–13(–14) μm in diameter. Meylan (1921) originally described this taxon (as *Comatricha laxa* var. *microcarpa*) from three collections made from the same tree in the Jura Mountains of Switzerland. Thus, these two collections appear to represent only the fourth and fifth known specimens and the first from the Western Hemisphere.

PARADIACHEOPSIS RIGIDA (Brândză) Nannenga-Bremekamp.—Butte Co.: Chico, corner of Arcadian and Sowilleno avenues, on palm stem in moist chamber, 17 Nov 1966, 3887; Chico, Lower Bidwell Park, on bark of *Juglans* sp. in moist chamber, 10 Jan 1977, *Whitney 295*; 2 mi ne. of Magalia, on bark of *Cupressus macnabiana* in moist chamber, 28 Oct 1978, *Whitney 1013*; Marin Co.: San Rafael, Lucas Valley Road and US Highway 101, on dead wood, 13 Jan 1977, *Whitney 248*. *Paradiacheopsis rigida* appears to be related most closely to *P. microcarpa*. Sporangia of the two taxa look very similar under a stereoscopic microscope. They can, however, be distinguished by numerous characters. In *P. rigida*, the sporangia attain 1.25 mm in total height; the base of the stipe is distinctly yellowish; most of the capillitium originates from the apex of the columella; the branches are dichotomous, flexuose, and occasionally anastomosed; and the spores are 9–10 μm in diameter and minutely spinulose. In *P. microcarpa*, however, the sporangia are smaller, rarely reaching 1 mm; the stipe is black along its entire length; the capillitium arises evenly along the length of the columella; the branches are extremely rigid, completely free, and not dichotomous; and the spores are 11–13(–14) μm in diameter and distinctly warted. *Paradiacheopsis rigida* has been reported in the United States only from Minnesota (Hagelstein 1944).

DIDYMIACEAE

DIDERMA EFFUSUM (Schweinitz) Morgan.—Alameda Co.: Berkeley, University of California Campus, on dead leaves and herbaceous

stems, *E. E. Morse*, 22 Jan 1930. This distinctive species is characterized by flat sporangiate to plasmodiocarpous fructifications that contain minutely warted spores with clusters of larger, darker warts. *Diderma effusum* is generally common throughout its worldwide distribution; therefore, it is interesting that I have never found it in over 20 years of collecting in California. This collection appears to be the only record for the state.

DIDYMIUM BAHIENSE Gottsberger. — Humboldt Co.: Trinidad, College Cove, on fallen leaves, 20 Apr 1973, 12753; Mendocino Co.: MacKerricher Beach State Park, on dead leaves, 29 Dec 1967, 7629, 7641; Albion, on fallen leaves, 11 Apr 1968, 8205, 8225. This species was originally described from Brazil (Gottsberger 1968) and has been reported from the Netherlands (Nannenga-Bremekamp 1972) and England (Mitchell 1977). These collections appear to be the first reports from North America. The features that delineate this taxon are the yellowish stipes, the distinctive whitish to yellowish pseudocolumellae, and the minutely warted spores with clusters of larger, darker warts. It appears to be similar to *D. megalosporum* Berkeley & Curtis, but in that species the pseudocolumella is usually spiny or roughened and the spores lack the distinct clusters of larger and darker warts.

DIDYMIUM VERRUCOSPORUM Welden. — Butte Co.: Chico, Upper Bidwell Park, on dead grass leaves, 17 Jan 1969, 9828; Glenn Co.: 13 mi s. of Hamilton City, on dead dicot leaves, 24 Feb 1968, 7861, 7864. The nodding, globose sporangia containing white, globose columellae and warted spores with clusters of larger warts easily separates this species from others in the genus. *Didymium verrucosporum* was described originally from Panama (Welden 1954) and has been found in various European and Asian localities. These collections appear to be new records for the United States. The California material differs from the type in that, in addition to the warts, the spores bear a wide-meshed reticulum with four or five meshes per spore. The reticulum is very similar to the one illustrated for *Didymium nigrisporum* by Nannenga-Bremekamp et al. (1984).

LEPIDODERMA AGGREGATUM Kowalski. — Tehama Co.: Wells Cabin Campground, 6300 ft., on decaying bark near the melting snow, 18 Jun 1966, 3570. This distinctive alpine slime mold is characterized by sessile, clustered, buff sporangia 1.5–3.0 mm in diameter, which contain spores with widely scattered spines. Until now, it was known only from the state of Washington, where it is extremely common in the spring near melting snowbanks.

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COLD TOLERANCE IN THE DESERT FAN PALM, *WASHINGTONIA FILIFERA* (ARECACEAE)

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ABSTRACT

Natural populations of *Washingtonia filifera* tolerate temperatures down to -11°C and subfreezing temperatures for at least 22 hours. Nonacclimatized seedlings survive temperatures as low as -21°C for one hour. Seeds are hardy, germinating readily after 36 hours of exposure to a temperature of -21°C . Available climatic data suggests that the absence of *W. filifera* from springs and seeps in the eastern Sonoran Desert and portions of the Mojave Desert is for reasons other than simple intolerance to subfreezing temperatures.

The desert fan palm, *Washingtonia filifera* (Lindl.) Wendl., of the Sonoran Desert is known to tolerate subfreezing temperatures. Muirhead (1961) stated that adults survived temperatures to at least -9°C with small plants showing leaf burn at temperatures below -4°C . Blombery and Rodd (1982) believed that desert fan palms survived winter temperatures down to -5°C . Although these references provide some information on the minimum temperature tolerance of *W. filifera*, no data have been presented on the duration of the subfreezing temperatures. The purpose of this paper is to present 1) new information on the minimum temperatures and the duration of subfreezing temperatures tolerated by natural populations of *W. filifera*, and 2) the results of tests on the cold tolerance of both seeds and seedlings. I use these data to evaluate the effect of temperature on the present distribution of *W. filifera* (Fig. 1).

METHODS

Minimum temperatures that occurred in the vicinity of six palm oases were obtained from seven meteorological shelters within the Sonoran Desert of southeastern California and western Arizona [Agave Hill, Pinyon Crest, and Taylor Site data obtained from the Boyd Deep Canyon Desert Research Center, Palm Desert, CA; Kofa and Castle Creek data from Sellers and Hill (1974); Oasis of Mara data obtained from Joshua Tree National Monument Headquarters; Indio data from U.S. Date and Citrus Station (1981)]. Locations of oases and shelters are given in Table 1. With two exceptions, each palm oasis was situated within 2 km and at approximately the same elevation as one of the weather shelters. Owl Hole was approximately

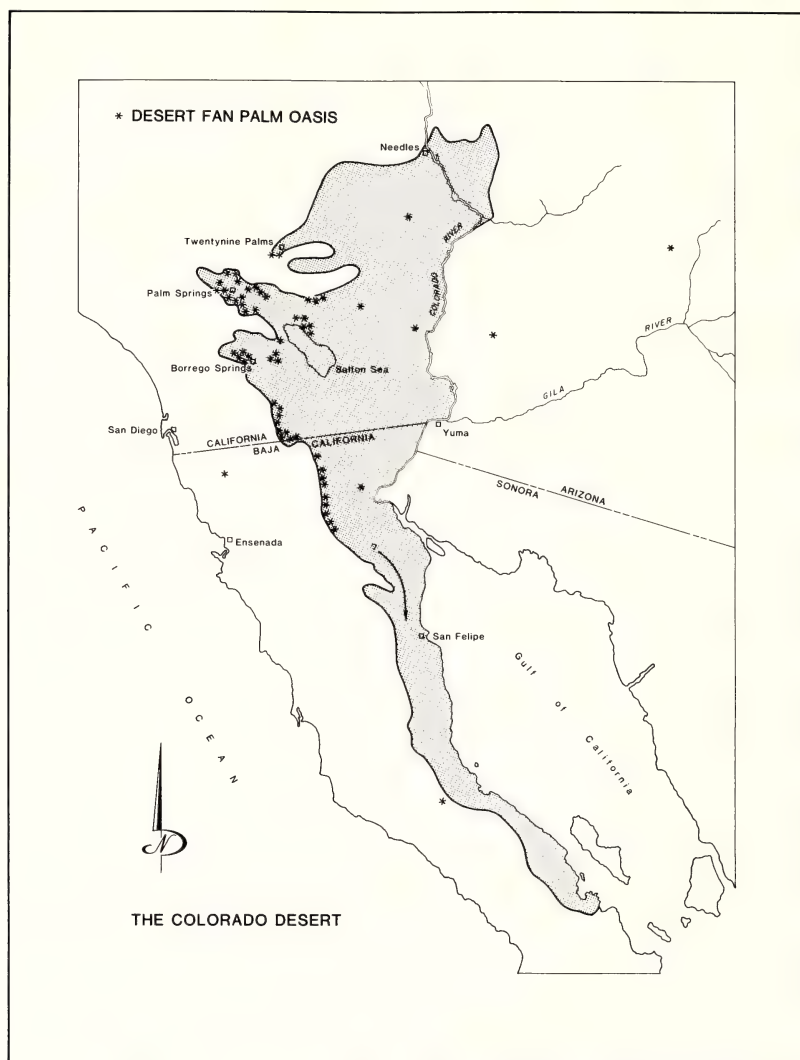


FIG. 1. The Colorado Desert subdivision of the Sonoran Desert (shaded area). * = location of desert fan palm oases.

40 m higher and 7 km north of the weather shelter at Indio, Riverside Co., CA. Kofa Palm Canyon was 144 m higher and 12 km north of the weather shelter located in the settlement of Kofa, Yuma Co., AZ. Three of the shelters (Agave Hill, Taylor Site, and Pinyon Crest) enclosed continuous recording thermographs and, thus, recorded the duration of subfreezing temperatures.

Minimum cold tolerance of *W. filifera* seeds was determined by

TABLE 1. MINIMUM TEMPERATURES AND DURATION OF SUBFREEZING TEMPERATURES EXPERIENCED BY POPULATIONS OF *Washingtonia filifera* IN SIX PALM OASES LOCATED IN THE SONORAN DESERT. D = duration; BDCDRC = Boyd Deep Canyon Desert Research Center, Univ. California, Riverside.

Min. temp. °C	D (h)	Palm oasis location	Elevation (m)	Date of minimum	Shelter location
-03	15	CA, Riverside Co.: Santa Rosa Mountains, Hidden Palms Canyon	938	28 Jan 1979	CA, Riverside Co.: BDCDRC, Agave Hill
-04	14	Hidden Palms Canyon	938	2 Jan 1974	Agave Hill
-04	14	CA, Riverside Co.: Santa Rosa Mountains, Dos Palmas Spring	1066	20 Jan 1983	CA, Riverside Co.: BDCDRC, Pinyon Crest
-05	?	AZ, Yuma Co.: Kofa Palm Canyon	685	?	AZ, Yuma Co.: Kofa
-06	18	Dos Palmas Spring	1066	29 Dec 1982	Pinyon Crest
-08	?	AZ, Yavapai Co.: Castle Creek	621	?	AZ, Yavapai Co.: Castle Hot Springs
-09	22	Dos Palmas Spring	1066	29 Jan 1979	BDCDRC, Taylor Site
-11	?	CA, San Bernardino Co.: Joshua Tree Nat. Mon., Oasis of Mara	600	3 Jan 1974	CA, San Bernardino Co.: Twentynine Palms, Mon. Headquarters
-11	?	CA, Riverside Co.: Indio Hills, Owl Hole	37	22 Jan 1937	CA, Riverside Co.: Indio

placing them in a freezer for the durations and temperatures shown in Table 2. Following cold exposure, the seeds were planted in plastic containers filled with a mixture of compost and vermiculite in equal proportions. The containers were placed on a heating pad that maintained a constant temperature of 32°C. The bedding medium was saturated with water on alternate days. Daily inspections were made

TABLE 2. DURATION OF MINIMUM TEMPERATURE EXPOSURES OF *Washingtonia filifera* SEEDS.

Min. temp. °C	Duration (h)	Germination success #/total	%
-07	24	38/40	95
-07	96	18/20	90
-12	06	38/40	95
-21	36	17/20	85

TABLE 3. DURATION OF MINIMUM TEMPERATURE EXPOSURES OF *Washingtonia filifera* SEEDLINGS.

Min. temp. °C	Duration (h)	Survival rate #/total	%
-12	1.0	6/20	30
-12	3.0	0/19	0
-12	6.0	0/19	0
-18	0.5	20/20	100
-21	1.0	4/19	21

to determine whether sprouting had occurred. Cold tolerance of seedling palms was determined by placing 20–30 day-old sprouts in a freezer for the durations and temperatures shown in Table 3.

RESULTS

Weather records indicate the minimum temperature tolerance of natural populations of *W. filifera* to be at least -11°C , two degrees lower than the known minimum of -9°C (Table 1). In addition, it appears that adult trees can withstand up to 22 h of subfreezing temperatures.

Palm seeds germinated readily after exposure to subfreezing temperatures. In these studies, seeds tolerated exposures as low as -21°C for 36 h (Table 2). Seeds exposed to such low temperatures also tended to germinate earlier ($\bar{x} = 21.5$ days; s.d. = 2.6) than seeds not exposed to subfreezing temperatures ($\bar{x} = 27.5$ days; s.d. = 5.1). These means are significantly different (t-test, $p < 0.001$). Seeds also germinated readily following exposure to freezing temperatures for seven days with temperatures dropping to -30°C (A. Stumpf, pers. comm.). Palm seedlings were less tolerant of cold, although four seedlings survived one hour exposure at -21°C (Table 3). Percent survival may have increased had the seedlings been acclimatized prior to exposure to freezing temperatures.

DISCUSSION

At least three populations of *W. filifera* probably experience even colder temperatures and for longer durations than do the palm oases listed in Table 1. Fortynine Palms oasis in Joshua Tree National Monument is located 6 km west of the Oasis of Mara and 206 m higher at 878 m. Because of its higher elevation and decreased exposure to direct sunlight due to its canyon location, temperatures are probably colder for longer periods at Fortynine Palms than at the Oasis of Mara. Mopah Spring, located in the Turtle Mountains of San Bernardino Co., CA, lies 24 km north and 100 m higher than the Oasis of Mara. Some individuals in Munsen Canyon (Joshua

Tree National Monument) occur at approximately 1015 m, which is the second highest elevation recorded for adult *W. filifera*. Although no climatic data exist for this site, the upper end of the Munsen Canyon palm grove may experience colder temperatures than do the high-altitude palms at Dos Palmas Spring in the Santa Rosa Mountains.

Low winter temperature is a probable factor in the exclusion of *W. filifera* from certain regions adjacent to its present range. Desert fan palms line many of the eastward-trending canyons that drain the Peninsular Ranges of southern California and adjacent Baja California Norte. Perennial streams exist in over a dozen of these canyons. Palms occur at the lowest point where water appears on the surface and they grow along the streams up to an elevation of approximately 900 m; they are absent above 1000 m even though the streams continue well above this elevation. Palms also are absent from most of the Mojave Desert where winter temperatures occasionally drop to -13°C or lower (U.S. Weather Bureau 1951, 1980, Sellers and Hill 1974). These observations, combined with the data from Table 3, suggest that the distribution of *W. filifera* is affected by low winter temperatures, but not to the degree that the tropical association of its family might indicate. How cold temperatures affect the palms is not known. Possibly, the seedlings may fail to establish because of a reduction in competitiveness that results from retarded growth or because of frost damage to the apical meristem.

The information presented on low temperature tolerances of *W. filifera* indicates, insofar as temperature is concerned, that the distribution of this species could be broader than it is at present. For example, there are no low temperature records that preclude the widespread occurrence of desert fan palms at springs and streams within the Sonoran Desert of Arizona and northern Mexico (Sellers and Hill 1974, Steinhäuser 1979). The presence of two palm oases in Arizona, at the Kofa Mountains and Castle Creek, indicates that climatic conditions are suitable for *W. filifera* in the Sonoran Desert. Potential habitat also exists in the Colorado River drainage region of southern Nevada and the Death Valley area in the Mojave Desert. Geographical and ecological barriers, the lack of efficient dispersal agents, or insufficient time may account for the absence of the desert fan palm in these regions.

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ANNOUNCEMENT

NEW PUBLICATIONS

- COPE, E. A., *Native and cultivated conifers of northeastern North America: A guide*, Cornell Univ. Press, 124 Roberts Place, Ithaca, NY 14850, 1986, 231 pp., illus., ISBN 0-8014-1721-X, \$39.95 (hardbound), ISBN 0-8014-9360-9, \$17.95 (paperbound).
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PHOSPHORUS AND PH TOLERANCES IN THE
GERMINATION OF THE DESERT SHRUB
LARREA TRIDENTATA (ZYGOPHYLLACEAE)

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ABSTRACT

Seeds of *Larrea tridentata*, a dominant shrub of deserts in the southwestern U.S., were germinated on both a pH and phosphorus (P) gradient to determine if requirements for germination can help explain the field distribution of *Larrea*. Germination decreased significantly above pH 8, which is consistent with the conspicuous absence of *Larrea* from high pH sodic or saline desert soils. Although *Larrea* tends to be absent from noncalcareous soil, seed germination was not inhibited in acidic solutions. Germination showed no response to P or to interactions of pH and P. In contrast, recent literature has suggested that *Larrea* may be restricted to calcareous soils of low phosphorus availability due to toxicity of high concentrations of P to seedlings.

Larrea tridentata (Sessé & Moc. ex DC.) Cov. (creosote bush) is one of the most abundant and widely distributed shrubs of southwestern deserts (Runyon 1934); its limits have been used to define the warm desert region of North America (Benson and Darrow 1954). Within its range, however, *Larrea*-dominated communities often exhibit sharp boundaries, and a complete transition to other communities may be seen within 5–10 meters (Barbour 1969). Age distributions of *Larrea* in mature communities and observations of germination in the field indicate that germination and survival of seedlings are rare events under natural conditions (Barbour 1969, Ackerman 1979, Boyd and Brum 1983, Goldberg and Turner 1986) and suggest that germination could affect the distribution of *Larrea*.

Several authors have shown that soils in areas dominated by *Larrea* are porous and have greater drainage and aeration than do soils of adjacent areas (Yang and Lowe 1956, Fosberg 1940, Lunt et al. 1973). Others have observed that *Larrea* is found on soils that are generally calcareous throughout the profile (Hallmark and Allen 1975, Gardner 1958). *Larrea* apparently has no unusual physiological demands for calcium (Ca) (El-Ghonemy et al. 1978), but soil CaCO₃ may modify physical and chemical soil properties that are essential to the survival of *Larrea* (Hallmark and Allen 1975, Johnson 1961).

One potential effect of free CaCO₃ in soil is the fixation of available phosphorus (P) onto carbonates. Chemical interactions between Ca and P have been well documented, both in experimental solutions and in natural systems (Griffin and Jurinak 1973, Avnimelech 1983,

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Cole and Olsen 1959). Carbonates affect P levels in solutions through ion pairing with Ca, physical sorption, and the precipitation of calcium phosphate minerals (Marion and Babcock 1977). Fixation of P by soil carbonates may lower crop response to P fertilization in the southwest (McCaslin and Gledhill 1980, Chang 1953).

Musick (1978) found that P was toxic to *Larrea* seedlings at fairly low external concentrations ($10\ \mu\text{M}$) in slightly acid solution cultures (pH 6). Because there was no toxicity response at pH 8, Musick suggested that *Larrea* is adapted to alkaline, calcareous soils of low P availability. In a study of the germination requirements and tolerances of *Larrea* seeds, Barbour (1968) found no differences in germination success in the pH range of 7–10. Barbour, however, used phosphate buffers of an unreported P concentration to establish these solution pH values. In the light of Musick's (1978) finding of a significant effect of P in seedling growth, we have reevaluated the germination tolerance of *Larrea* with respect to both pH and various levels of P.

METHODS

Seeds of *Larrea tridentata* were collected in July 1984 from shrubs along a bajada of the Jornada Experimental Range of New Mexico State University near Las Cruces, New Mexico. Fruits from ca. 30 shrubs were mixed and stored in paper bags at room temperature until germination experiments began.

Experimental methods followed those of Barbour (1968), with several modifications. Whereas Barbour used whole mericarps in his germination trials, the high incidence of empty mericarps in our collections prohibited this technique. Mericarps were cracked open, and only mature seeds whose lengths were approximately 3 to 5 mm were used in the experiment.

Seeds were germinated along both a pH and a P gradient in a 2-way factorial design. The Modified Universal Buffer (MUB) of Skujins et al. (1963), a phosphate-free buffer used widely in phosphatase enzyme studies (Tabatabai and Bremner 1969), was used to establish the pH of the experimental solutions. Solutions of pH 7, 8, 9, and 10 were used as in Barbour (1968), as well as an additional treatment of pH 4.5. Buffers were mixed 1:1 with half-strength modified Hoagland's solution (Downs and Hellmers 1975) with a subsequent readjustment of pH. Treatment levels of P were 1) $1\ \mu\text{M}$, derived from the quarter-strength modified Hoagland's solution with no additional P added; 2) $10\ \mu\text{M}$; and 3) $100\ \mu\text{M PO}_4\text{-P}$, added as KH_2PO_4 . These concentrations span the range of P levels used by Musick (1978).

In each treatment, we used 100 seeds grouped into 5 lots of 20 seeds each. As in Barbour (1968), seeds were soaked for 3 hours in

TABLE 1. NUMBER OF SEEDS THAT GERMINATED AFTER 5 AND 10 DAYS IN EACH pH \times PHOSPHORUS TREATMENT. (abcde) values with the same letter within the pH \times phosphorus factorial cross on each day are not significantly different by Duncan's multiple range test (5% level). (ABC) values with the same letter for pH treatments on each day are not significantly different by Duncan's multiple range test (5% level). * = one-way ANOVA indicates no significant differences (5% level) between values for phosphorus treatments on each day.

Day 5				
pH	Phosphorus concentration			Mean over all phosphorus treatments
	1 μ M	10 μ M	100 μ M	
4.5	12.0 ^{bc}	15.8 ^a	14.4 ^{ab}	14.1 ^A
7	13.4 ^{abc}	11.6 ^{bc}	12.0 ^{bc}	12.4 ^A
8	13.8 ^{abc}	10.2 ^{de}	16.2 ^a	13.4 ^A
9	13.0 ^{abc}	8.0 ^{de}	8.2 ^{de}	9.7 ^B
10	4.8 ^c	6.8 ^{de}	6.8 ^{de}	6.1 ^C
Mean over all pH treatments	11.4*	10.5*	11.5*	
Day 10				
pH	Phosphorus concentration			Mean over all phosphorus treatments
	1 μ M	10 μ M	100 μ M	
4.5	15.8 ^{ab}	17.4 ^a	16.6 ^{ab}	16.6 ^A
7	15.0 ^{abc}	16.2 ^{ab}	14.4 ^{abcd}	15.6 ^A
8	16.6 ^{ab}	13.2 ^{bcd}	17.0 ^a	15.2 ^A
9	14.4 ^{abcd}	11.8 ^{cde}	11.4 ^{de}	12.5 ^B
10	8.6 ^c	8.6 ^c	8.8 ^c	8.7 ^C
Mean over all pH treatments	14.1*	13.4*	13.6*	

the appropriate treatment solution, and each set of 20 seeds was transferred to a petri dish filled with sand moistened with the same solution. All dishes were incubated in darkness at 25°C. We tallied germinations after both 5 and 10 days, and observed no germination after this period.

Statistical analyses were performed using the ANOVA procedure of SAS (SAS Institute Inc. 1982). The number of seeds that germinated in each lot of 20 seeds was treated as one observation. When the ANOVA indicated statistical significance, Duncan's multiple range test was used to distinguish differences among treatments.

RESULTS

Although pH had a significant effect on germination ($p < 0.0001$), there was no effect of P concentration (Table 1). There were no

significant differences in germination among pH 4.5, 7, and 8, but the number of seeds that germinated declined sharply at pH 9 and 10. The ANOVA for day 5 counts showed a significant interaction between pH and P ($p < 0.0004$), possibly due to a high mean germination value for pH 9 (1 μM $\text{PO}_4\text{-P}$ solutions) and a high value for pH 8 (100 μM solutions). The interaction was not significant on day 10, and we believe that it occurred as a result of random variation.

DISCUSSION

Differences in methodology may account for the disparity between our results and those of Barbour (1968), who found no effect of pH on germination over the range of pH 7–10. Although his germination trials lasted 5 days, we found significant germination occurring between 5 and 10 days in seeds extracted from mericarps. Barbour (1968) found that root growth decreased greatly with increasing pH, especially above pH 8. The response curve of root growth to pH (Fig. 5 in Barbour 1968) is remarkably similar to the response of germination to pH found in this study. The lack of response of germination to P concentration probably reflects the high internal stores of P in seeds of *Larrea* (Barbour 1968, Musick 1978). Thus, nutrient absorption does not become significant until seedling emergence.

Our data show that relatively acid solution (pH 4.5) did not inhibit the germination of *Larrea* seeds. Barbour (1968) found that root growth was greater in slightly acidic solutions (pH 6) than in those of higher pH. Thus, germination and early root development in response to pH cannot be used to explain the distribution patterns of *Larrea* found by Hallmark and Allen (1975), who showed that shrubs were restricted to soils that were calcareous in the upper 10 cm.

Solutions of pH 9 to 10 frequently reduced germination to less than 50% of maximum, certainly an important reduction for a species that has no significant seed bank (Boyd and Brum 1983) and few years that are favorable for germination and establishment in the field (Ackerman 1978). This result is consistent with known *Larrea* distribution patterns. Calcic soils have pH's in the range of 8–8.4, and soil pH will be higher only when significantly sodic or saline. *Larrea* is conspicuously absent from saline soils near topographic lows and playas (Barbour 1969, Fosberg 1940, Went and Westergaard 1949).

Many of the environmental variables that appear to affect *Larrea* distributions are correlated, and thus it is difficult to discern cause-and-effect relationships in nature. Calcareous soils tend to have a well-buffered pH range and are often coarse-grained with good in-

ternal drainage, whereas soils of a higher pH tend to be saline and fine-grained, with a lower permeability. Lunt et al. (1973) showed that *Larrea* has a relatively high oxygen requirement for root growth, and the correlation between CaCO_3 and *Larrea* occurrence may be due to the improved aeration and root penetration in CaCO_3 -rich soils rather than to the direct presence of CaCO_3 or to the buffering of soil pH by CaCO_3 (Lunt et al. 1973, Johnson 1961). Our data suggest that soil pH does not limit the germination of *Larrea* in acid, non-calcareous soils of southwestern deserts, although soil pH may interact with other factors to determine successful seedling establishment and growth.

ACKNOWLEDGMENTS

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ANNOUNCEMENT

NEW PUBLICATION

RZEDOWSKI, J. and G. C. DE RZEDOWSKI (eds.), *Flora Fanerogámica del Valle de México*, Vol. 2, *Dicotyledoneae (Euphorbiaceae-Compositae)*, Instituto de Ecología, AP 18-845, Deleg. Miguel Hidalgo, CP 11800, México, D. F., 1985, 674 pp., illus., ISBN 968-7213-02-7, US \$35.00 (hardbound). [The second volume of a proposed three-volume flora. Volume 1 (publ. Mar. 1979, reprinted 1984, 432 pp., US \$28.00, source above) provided introductory information on topography, geology, climate, plant communities, etc., and a floristic treatment of gymnosperms and of dicotyledons from Saururaceae to Polygalaceae. Volume 3 will include the monocotyledons.]

NOTEWORTHY COLLECTIONS

CALIFORNIA

MANNIA FRAGRANS (Balb.) Frye & Clark (HEPATICOPSIDA: AYTONIACEAE).—Tuolumne Co., mountain on n. side of Tioga Pass, Yosemite National Park, 10,000 ft, 4 Jul 1932, *M. S. Baker* 5809 (UC). Mono Co., H. M. Hall Natural Area near Stanford Research Area, T1N R24E S1, moist diffusely lit soil under boulder, in lodgepole pine forest and adjacent meadows, ca. 10,000 ft, 3 Jun 1977, *D. H. Norris* 48446 (HSC); Tioga Jct. Campground about 2.5 mi n. of Tioga Pass on hwy. 120, T1N R25E S19, moist, sunny soil between boulders, in open meadows and adjacent rock outcrops, ca. 9500 ft, 2 Jun 1977, *D. H. Norris* 48355 (HSC). Inyo Co., slopes above Treasure Lake, w. of Big Pine, T9S R31E S27, on temporarily moist, sunny soil at base of boulder, in alpine fell field with scattered *Pinus albicaulis*, ca. 11,500 ft, 6 Sep 1975, *D. H. Norris* 47006 (HSC, JE) (verified by R. Grolle, JE).

Previous knowledge. Eurasia; e. North America w. to Colorado, and perhaps Idaho and the Yukon (Schuster, American Midl. Nat. 59:274, 1958).

Significance. First records for CA. This species should be looked for farther n.; I have seen sterile specimens apparently belonging here from Modoc Co., CA and Josephine Co., OR (*Norris* 22473 and 52495, respectively, both HSC).

MYLIA ANOMALA (Hook.) S. F. Gray (HEPATICOPSIDA: JUNGERMANNIACEAE).—Humboldt Co., *Sphagnum* bog at Big Lagoon Co. Park, T9N R1W S13, near sea level, 2 Jun 1977, *D. H. Norris* 48316 (HSC).

Previous knowledge. Circumboreal, s. on the Pacific coast to WA (Schuster, The Hepaticae and Anthocerotae of North America East of the Hundredth Meridian 2:1040, 1969).

Significance. First record for CA.

PREISSIA QUADRATA (Scop.) Nees (HEPATICOPSIDA: MARCHANTIACEAE).—Siskiyou Co., Salmon River near Big Flat, T37N R9W S18, on moist sunny seepage on schistose wall of stream, ca. 5000 ft, 4 Aug 1968, *D. H. Norris* 9185 (HSC); in moist canyon along Jaynes Creek to headwaters (nw. of Klamath River), T47N R3W S13, very moist diffusely lit boulder along stream in white fir forest, ca. 5000–6000 ft, 10 Jul 1977, *D. H. Norris* 48690 (HSC). Mono Co., meadow above Lake Mildred, Convict Creek drainage, 118°52.3'W, 37°32.6'N, bedrock limestone, 9800 ft, 20 Sep 1981, *A. T. Whittemore* 1496 (DAV), 1498A (CAS), 1516 (to be distributed), 1521 (to be distributed), 1540 (CAS).

Previous knowledge. Circumboreal, s. in the Pacific states to OR (Hong, Bryologist 81(3):441, 1978).

Significance. First records for CA.

MEXICO

ATHALAMIA HYALINA (Sommerf.) Hatt. (HEPATICOPSIDA: CLEVEACEAE).—Nuevo Leon, Puente de Dios, ca. 8 km n. of Galeana on road to Rayones, 100°05.5'W, 24°53'N, sheltered grotto in canyon wall, arid scrub with *Cupressus*, 1500 m, 27 Aug 1984, *A. T. Whittemore* 2469, *M. Lavin*, and *T. Atkins* (MEXU).

Previous knowledge. Circumboreal, s. in the Rocky Mountain system to CO and AZ (Schuster, Amer. Midl. Nat. 59:298, 1958, as *Clevea hyalina*).

Significance. First record for Mexico.

RICCIA ALBIDA Sull. (HEPATICOPSIDA: RICCIACEAE).—Nuevo Leon, junction of Monterrey bypass and hwy. 40, ca. 16 mi w. of Monterrey, 100°33.5'W, 25°42'N, rather

open soil near shrubs, low land above banks of river, in thorn scrub, 880 m, 12 Mar 1982, *A. T. Whittemore 1599, T. Ayers, F. Barrie, and D. Lemke* (MEXU).

Previous knowledge. Edwards Plateau of Texas (McGregor and Menhusen, *Bryologist* 64:71–74, 1962) and e. LA (Guerke, *Bryologist* 74:203, 1971).

Significance. First record for Mexico.

CAMPYLIUM HALLERI (Hedw.) Lindb. (BRYOPSIDA: AMBLYSTEGIACEAE).—Nuevo Leon, cliffs just ne. of the microwave station, summit of Cerro Potosi, ca. 17 km nw. of Galeana, 100°14'W, 24°52½'N, on rock of cliff in *Pinus hartwegii* forest, 3700 m, 23 Aug 1984, *A. T. Whittemore 2373, M. Lavin, and T. Atkins* (MEXU) (verified by C. Delgadillo M., MEXU).

Previous knowledge. Circumboreal, s. in the Rocky Mountains to CO (Crum & Anderson, *Mosses of Eastern North America*, p. 947, 1981).

Significance. First record for Mexico.

ENTODON SCHLEICHERI (Schimp.) Demeter (BRYOPSIDA: ENTODONTACEAE).—Nuevo Leon, on road up Cerro Potosi 1.5 mi below the lower microwave tower, ca. 17 km nw. of Galeana, 100°13.5'W, 24°53'N, on rock in grove of *Populus tremuloides*, *Pinus-Abies* forest with grazed herbaceous understory, 3100 m, 24 Aug 1984, *A. T. Whittemore 2396, M. Lavin, and T. Atkins* (MEXU, CAS).

Previous knowledge. Eurasia and Lincoln Co., NM (Buck & Crum, *Bryologist* 81: 429–432, 1978).

Significance. First record for Mexico.

TIMMIA MEGAPOLITANA Hedw. subsp. *BAVARICA* (Hessl.) Brassard (BRYOPSIDA: TIMMIACEAE).—Coahuila, atop high cliffs on n. side of summit of Sierra Coahuilón, ca. 25 km (by air) e. of San Antonio de las Alazanas, 100°20'W, 25°15'N, in rock crevice beneath overhang in open *Pinus-Picea* forest with *Lupinus* and *Senecio* on soil and *Heuchera* on rock faces, 3500 m, 23 Jul 1985, *A. T. Whittemore 2686, A. McDonald, S. Boykin, and S. Ginzburg* (MEXU, CAS, TEX) (verified by C. Delgadillo M., MEXU).

Previous knowledge. Circumboreal, s. in the Rocky Mountains to CO and AZ; also a single collection from the state of Mexico, Mexico (Brassard, *Lindbergia* 10:33–40, 1984).

Significance. Fills in a gap of almost 2000 km between the single Mexican report and the nearest sites in the s. Rocky Mountains.—ALAN T. WHITTEMORE, Dept. of Botany, Univ. of Texas, Austin 78712.

REVIEWS

Flora of the Santa Monica Mountains, California. By PETER H. RAVEN, HENRY J. THOMPSON, and BARRY A. PRIGGE. Southern California Botanists, Special Publication No. 2. Second Edition, June 1986. \$8. (paperbound).

This flora was published first in 1966 as an introductory manual for beginning students at UCLA, etc. and was revised in 1977. Since 1966, 72 species have been added, of which 45 are native, now bringing the total to 880 species. A major revision was undertaken by the junior author, Barry A. Prigge, and resulted in many nomenclatorial changes in the species, genera, and even at the family level.

There is a map of the Santa Monica Mountains, a special area close to some five million people. Concerned citizens have set aside many local government parks, including 33,000 acres in State Parks and 70,000 acres as a National Recreation Area.

The introduction follows with an in-depth explanation of the Mediterranean climate, and a summation of the geology. The vegetation is ably discussed with black and white photographs and a table of Raunkiaer's life forms. There is a statistical summary of the flora. The catalogue is alphabetical, with families at the top of each page for easy reference, an asterisk before introduced species with countries of origin, and numbers for months indicating the flowering periods. A glossary is added with an extensive list of literature cited, and an index is included.

The main part of the flora has ample keys to the divisions, classes, families, genera, and species of vascular plants. Obvious characters are used to simplify the keys when applicable and they are not unduly technical unless needed. The local distribution is usually given in an easy flowing simple declarative sentence. A few are vague: *Lepidospartum squamatum* (A. Gray) A. Gray is quoted as "Occasional in coastal sage scrub and southern oak woodland", . . . ending with "Often in washes and along streams in sandy soil." In my opinion, this plant is rarely found outside washes in a given plant community. I would like to see every plant with an exact habitat(s) when possible. The authors shine here and there with such descriptions as "shallow soil over rocks in open grassland"; I then know that they know about this specific plant. Synonyms are given for many taxa, although I would like to see more in a scientific publication such as this. A few typographical errors occur here and there besides the included errata sheet.

When I read about special taxa that literally shoot up out of the pages as disjunct species, etc., without an explanation, I am left with a void. Nothing is given about *Asplenium vespertinum* Maxon, *Lewisia rediviva* Pursh var. *rediviva*, *Silene verecunda* S. Watson subsp. *platyota* (S. Watson) Hitch. and Maguire, *Myrica californica* Cham., *Perityle emoryi* Torr., *Adenostoma sparsifolium* Torr., *Batis maritima* L., etc. But I can see why. Most of these field notes are in McAuley (1985).

Another minor criticism but important to me is the use of "extinct" and "extirpated" without historical data. Under *Astragalus pycnostachys* A. Gray var. *lanosissimus* (Rydb.) Munz and McBurne ex Munz (a plant that I have heard and wondered about for years along the seaward side of the Santa Monica Mountains), I read "Very rare if not already extirpated from our area; not actually known in our area but may occur at Mugu Lagoon." This gives me mixed reactions. Why not shorten this to the facts by merely citing the last collection(s), e.g., a hypothetical case: "Last collected by Parish at Pt. Mugu in 1901," and not seen since. Then one can speculate where one might look for it. An interesting entry is *Myrica californica* Cham. and Schlecht. "Presumably in tangled streamside vegetation; Santa Monica Canyon." This same explanation is in the 1966 flora. It seems like someone would have checked this out in 20 years. McAuley (1985) states it is "Found in canyons and moist slopes at low elevations. Uncommon."

Now, to bring this flora into perspective. The Santa Monica Mountains have been of much interest to me because I became involved in a flora to the immediate north and was interested in the relation of the plants of the Santa Monica Mountains to the northern Channel Islands, because they are visually an extension of this range. I was first introduced to its flora by correspondence with Henry L. Bauer of Santa Monica Junior College, who was also interested in these mountains and published (mimeographed) in 1952 a "Check List and Distribution of the Plant Species Growing Naturally in the Santa Monica Mountains, California", by O. H. Kappler, consisting of 13 pages. In 1983, several popular checklists on the flora of the Santa Monica Mountains were published by Bob Muns, and in 1985 the *Wildflowers of the Santa Monica Mountains* by Milt McAuley appeared with 544 pages and 496 colored plates, followed in 1986 by *Flowering Plants: the Santa Monica Mountains* by Nancy Dale, with 239 pages and 214 colored plates. These two beautiful publications are irrevocably woven into this article.

I have the impression that cooperation is uncoordinated among the leading floristic authors, plant collectors, and the professional botanists. Barry Prigge states that for new species to be incorporated in future revisions, "Voucher specimens have to be made with collection data and deposited at a local herbarium." Several McAuley species are not listed as he (Prigge) has not seen them. Bob Muns in an October 1983 checklist states "I have found 20 more species growing in the Santa Monica Mountains." We in Santa Barbara also are guilty and can add two more species, *Lavatera arborea* L. and *Nicotiana clelandii* Gray. *Cordylanthus maritimus* Nutt. ex Benth. subsp. *maritimus* has been surveyed at the Mugu Lagoon by Julie M. Vanderwier and Judith C. Newman (Madroño 31:185-186. 1984), and others.

This flora is the only publication for these mountains with dichotomous keys and should remain the "scientific master list". It can only grow in scope with the help of many who have diverse interests. —CLIFTON F. SMITH, Santa Barbara Botanic Garden, 1212 Mission Canyon Rd., Santa Barbara, CA 93105.

Marcus E. Jones: Pioneer Western Geologist, Mining Engineer & Botanist. By LEE W. LENZ. xv + 486 pp., 9 pp. black and white photographs. Rancho Santa Ana Botanic Garden, Claremont, CA. 1986. ISBN 0-9605808-2-4, \$28.00 plus tax and \$1.50 shipping.

If Lee Lenz had done no more than compile and make generally available the excellent gazetteer of his subject's collecting localities and chronology for nearly a half century of field work, the botanical community would be greatly in his debt. For anyone who, like this reviewer, tends to identify Marcus E. Jones, A.M., solely with the Great Basin, the map on page 292 is a revelation, showing that he was active in every western state but Alaska and Hawaii, although his coverage was considerably more modest than his claims. His unconsummated "Flora of the Great Plateau" was to have embraced "the region west of the Plains" and extend well into both Canada and Mexico, in short, the American West.

But the author also has assumed the task of presenting a biography of Jones. This is a difficult assignment because the man and the scientist have become almost obscured by his reputation as a choleric, fiercely independent, feisty, rough-and-tumble combatant in a notably polemic era. Lenz allows Jones to speak for himself, but this does little to dispel the reputation. Jones was a born-again Protestant and frequently a lay preacher, but he was notably lacking in the Christian virtues of humility and charity. His strong religious commitment, however, did not pose an obstacle to his full acceptance of evolution, as it did for many of his contemporaries. The panoply of Nature was God's handiwork.

Born in Ohio, educated to a Master's degree at Iowa College (predecessor of Grinnell), he was prepared to teach Classics or, as was the custom in the West of his day, any other subject for which there was an opportunity. His precarious health drew him to outdoor life and his inclination to a career as a field naturalist. He did not succeed in establishing a firm institutional connection until late in life. He and his family, centered after 1880 in Salt Lake City, endured a grinding hand-to-mouth existence based on his irregular teaching assignments, preaching, free-lance writing on a variety of issues, and, increasingly, geological consulting. Mining investments seldom proved profitable and his performance as an expert witness for the prosecution in smelter-pollution law suits, while admirable, was not financially rewarding. His long-suffering wife augmented or supplied the family income with kindergarten teaching and operation of a rooming and boarding house.

Jones' most productive period botanically was undoubtedly from about 1880 to 1912. Every summer was devoted to collecting somewhere in the West, the winters to identifying, labeling, and distributing the resulting specimens for sale, and working on his "Flora." By 1885, access to the few existing botanical journals had been cut off, as it was to anyone who refused to have his proposals approved by members of the Eastern establishment. Launching of the journal *Zoë* by the Brandegees' provided

the opportunity to initiate his extensive series of "Contributions to Western Botany" in 1891, but a few years later he was doing his own publishing. The "Flora" was planned to be the first fully illustrated botany of the area. The manuscript for volume one was essentially completed by 1907, but the second remained incomplete, and there is no indication that he worked on it after he left Utah for California in 1923. Neither volume was ever published, and a "Trees and Shrubs of Utah" and a substantial "Flora of Flathead Lake" also remained in typescript.

Because Jones published relatively little of substance besides new species and trained no disciples, the book inevitably becomes in large part the history of his herbarium. By sale of collections, diversification of teaching stints, and consulting trips, he was able to cover an astonishing amount of territory, and amass a steadily growing private herbarium, which was clearly his first priority. From the early seventies until his death in 1934, he was continuously and vigorously adding specimens. Much of his concern in later years was finding a suitable home for it and, for the few active years remaining, for himself. In this he fortunately was successful. After brief flirtations with the California Academy of Sciences and the University of Utah, the herbarium was obtained for Pomona College by Phil Munz. Although terms of the sale provided for Jones to publish his "Flora", and he was now freed of financial worries for the first time in his life, much of the original area of his interest had long been preempted by other authors. He turned instead to field work in northern Mexico—further adding to his herbarium.

The author attempts a "summing up" of Jones' contributions, which particularly pairs him with Greene. Certainly the two were fellow mavericks and adepts at inventing colorful invective and generating hostility, but I think a closer comparison might have been made between Jones and Katharine Brandegee, whom he so greatly admired. Both had considerable gifts of critical analysis, but their special insights largely died with them.

The volume includes a list of published writings, diary and field notes, 1894 (Appendix I), the 112-page annotated gazetteer (Appendix II), and a list, with explanatory notes, of the nearly 800 new taxa that Jones proposed during his lifetime (Appendix III).

Incorporation of the Jones Herbarium into the Pomona-Claremont-Rancho Santa Ana research complex at last provides its creator the central role in West American botany that he never quite succeeded in attaining in life.—LINCOLN CONSTANCE, Dept. Botany, Univ. California, Berkeley 94720.

Botanical Illustration: Preparation for Publication. By NOEL H. HOLMGREN and BOBBIE ANGELL. 74 pp. The New York Botanical Garden, Bronx, NY 10458. 1986. ISBN 0-89327-272-8, \$12.

A quote the authors use in the beginning of this book could just as well apply to the authors themselves: "Well-ordered presentation is the sign of a well-ordered mind" (Alfred A. Blaker, 1977). This book is small, but it covers concisely and thoroughly all aspects necessary to produce a botanical illustration that is correct and aesthetically pleasing. I have done quite a bit of botanical illustrating, yet I was able to learn from this book. Holmgren and Angell not only cover basic illustrating guidelines, they also offer shortcuts and technical tips that can save both the illustrator and the author valuable time, money and energy.

Much has been written about scientific illustration (some of the better publications are included in a helpful Annotated Bibliography at the end of this book), but very little good information exists on the very special needs encountered in botanical drawings. From the first chapter, "Working Relationships", through others that include some useful information on tools, sizes and proportions of plates (including instruction on reductions), labels, captions, illustrations, maps and graphs, photographs and halftones, to preparing art for shipping, this volume contains a wealth of information in a very succinct and informative way. There is a good section on the

U.S. Copyright law that was changed in 1978. An understanding of this law is important, especially if either the artist or the author have any interest in maintaining rights to the artwork.

The illustrations used throughout the book are clear and nicely done. I thought the samples used in the chapter on "Plant Illustrations" were especially well-rendered. It's nice to see that the authors are quality artists as well as good writers. Their writing style is straight-forward and very clear; they stay away from verbal embellishments that might only tend to confuse. The Table of Contents is well done, making it a simple matter to look up particular information (chapters are indicated in bold type, whereas sub-headings with page numbers show specific areas contained in those chapters).

In short, this book would be a welcome addition to any botanist's or artist's library. Botanists who do their own illustrating will find this book especially helpful. — MAGGIE DAY, Dept. Biological Sciences, Univ. California, Santa Barbara 93106.

ANNOUNCEMENT

NEW PUBLICATIONS

VAN BRUGGEN, T., *The vascular plants of South Dakota*, 2nd ed., Iowa State Univ. Press, 2121 S. State Ave., Ames 50010, 1985, xxv, 476 pp., illus., ISBN 0-8138-0650-X, \$28.95 (paperbound). [First edition 1976; treatment of 1608 native and adventive species found in South Dakota and adjacent areas.]

SCAGEL, R. F., D. J. GARBARY, L. GOLDEN, and M. W. HAWKES, *A synopsis of the benthic marine algae of British Columbia, northern Washington and southeast Alaska*, Dept. of Botany, Univ. British Columbia, Vancouver V6T 2B1, 1986, vi, 444 pp., ISSN 0831-4861, ISBN 0-88865-460-X, Can \$15.00 (paperbound).

STUBBENDIECK, J., S. L. HATCH, and K. J. HIRSCH, *North American range plants*, 3rd ed., Univ. Nebraska Press, 901 North 17th St., Lincoln 68588, 1986, xv, 465 pp., illus., ISBN 0-8032-9162-0, \$18.95 (paperbound).

ANNOUNCEMENT

NEW PUBLICATIONS

COOKE, W. B., *The fungi of our mouldy earth*, Beihefte zur Nova Hedwigia, heft 85. J. Cramer, Berlin, West Germany, 1986, vi, 468 pp., 114 figs., 2 pl. [This volume includes chapters on the collection, preparation, isolation, and identification of fungi, in addition to those on habitats, classification, and a systematic list of the species.]

WELSH, S. L., N. D. ATWOOD, L. C. HIGGINS, and S. GOODRICH, *A Utah flora*, Great Basin Naturalist Memoir 9, Brigham Young Univ., 290 M. L. Bean Life Science Museum, Provo, UT 84602, 1986. [*A Utah flora* is a comprehensive treatment of the vascular flora of the state, including 2572 native species, 355 intraspecific entities, and 580 introduced species. Taxa are described, ecological data are given, and geographic information is provided.]

WIARD, L. A., *An introduction to the orchids of Mexico*, Comstock Publ. Assoc., Cornell Univ. Press, Ithaca, NY 14850, 1986, 216 pp., 80 pls. (color), ISBN 0-8014-1833-X, \$75.00 (hardbound). [A sampling, in 21.6 × 28 cm format, of 154 of the over 800 native orchid species of Mexico; all 154 species are illustrated by Wiard, mostly from plants in the wild or from collections of Wiard and friends. The main part of the book describes the 60 genera treated, with species descriptions giving habitat and other details.]

ANNOUNCEMENT

FIFTH WILDLAND SHRUB SYMPOSIUM

The Shrub Research Consortium is sponsoring the Fifth Wildland Shrub Symposium 30 June–2 July 1987 at Utah State University, Logan, Utah. The symposium, “Shrub Ecophysiology and Biotechnology”, will feature invited and contributed papers. Contributed presentations will be 20 minutes. The proceedings will be published by the USDA Forest Service Intermountain Research Station. If you would like to present a paper, send a title and abstract by 31, March 1987, to: Dr. Arthur Wallace, Laboratory of Biomedical and Environmental Sciences, UCLA, 900 Veteran Avenue, Los Angeles, CA 90024.

To receive preregistration materials and information please contact: Michael B. Price, Eccles Conference Center, Room 103 F, Logan, UT 84322-5005; phone: (801) 750-1696.

ANNOUNCEMENT

THIRD CALIFORNIA ISLANDS SYMPOSIUM

Hosted by

Santa Barbara Botanic Garden (SBBG), Santa Barbara Museum of Natural History (SBM), and the Southern California Academy of Sciences.

This symposium took place in Santa Barbara on 2–6 March 1987. Contributed papers covered the following topics: history and resource management; birds; fishes and marine botany; anthropology; oceanography; terrestrial and marine invertebrates; terrestrial botany; marine and terrestrial vertebrates; and geology and geography. A collected set of full length manuscripts and extended abstracts of papers presented at the symposium will be published in book form. For information concerning the event contact Dr. F. G. Hochberg, Santa Barbara Museum of Natural History, 2559 Puesta del Sol Rd., Santa Barbara CA 93105.

ANNOUNCEMENT

ELEVENTH GRADUATE STUDENT MEETINGS

The California Botanical Society will sponsor the Eleventh Graduate Student Meetings on 25, 26 April 1987 at the University of California, Davis.

The presentation categories (proposed research, research in progress, and finished research) allow for the sharing of ideas and knowledge among the graduate student community. Awards for each of these categories will be presented at the banquet on 26 April.

For information contact Niall F. McCarten, Graduate Student Representative, Dept. of Biology, San Francisco State Univ., 1600 Holloway, San Francisco, CA 94132.

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At the time of submission, authors must provide information describing the extent to which data in the manuscript have been used in other papers that are published, in press, submitted, or soon to be submitted elsewhere.



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January 26, 1987

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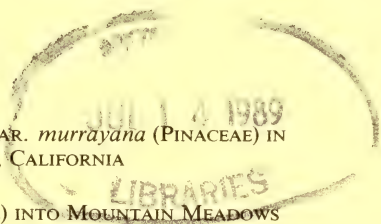
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MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

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GERMINATION AND ESTABLISHMENT OF
PINUS CONTORTA VAR. *MURRAYANA* (PINACEAE)
IN MOUNTAIN MEADOWS OF YOSEMITE
NATIONAL PARK, CALIFORNIA

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ABSTRACT

Pinus contorta var. *murrayana* (lodgepole pine) commonly invades mountain meadows. Studies were made on a wet and a dry meadow in Yosemite National Park, California, to determine differences in meadow habitat as defined by differences in composition and cover of herbaceous vegetation, soil characteristics, and physiography. Site ordination identified species on sites of decreasing moisture content. In both fall and spring, *P. contorta* seeds were sown on both covered and uncovered plots in each of 12 meadow sites. Germination and survival of seeds were measured for three consecutive years. Invasion of pine was uncommon on both the wetter meadow, dominated by *Aster alpigenus*, *Carex nebraskensis*, and *Deschampsia caespitosa*, and on the driest sites characterized by *Lupinus confertus* and *Horkelia fusca* subsp. *capitata*. Most invasion occurred on moderately dry sites dominated by *Aster occidentalis*, *Trifolium longipes*, and *Danthonia californica*. Differences in germination from fall and spring seeding were not significant. Depredation by rodents and birds reduced germination and survival on the uncovered seed plots by approximately 50%.

Pinus contorta Dougl. ex Loud. var. *murrayana* (Grev. & Balf.) Engelm. (lodgepole pine) commonly invades mountain meadows in the Sierra Nevada of California. Invasion is sporadic and the factors that limit germination and establishment of pine seedlings in meadows are not well understood. The invasion is important in meadow succession and is of concern to resource managers who are responsible for meadow conservation and management.

Mountain meadows differ substantially in topography, water availability, and microclimate. These differences occur as within- and between-meadow variation in timing of snow melt, drainage patterns, and vegetative cover. These factors probably also influence the timing and extent of lodgepole pine seedling establishment in meadows.

Germination of lodgepole pine is abundant in full sunlight, on bare mineral soil or disturbed duff, in the absence of competing

vegetation, and with adequate soil moisture (Lotan 1964, Shepperd and Noble 1976, Lotan and Critchfield in press). Seedling mortality is associated commonly with high soil surface temperature, drought, soils with low water-holding capacity, unincorporated organic matter, and grazing (Cochran 1969, Lotan and Perry 1977, Lotan and Critchfield in press). Specific sites within meadows that are more favorable for pine establishment are indicated by the presence of 'outlier' trees. These trees are associated commonly with exposed rocks, logs, and groups of shrubs (Leonard et al. 1968, 1969) that are thought to provide higher soil temperature, more favorable soil texture and drainage, earlier snow melt, and protection from browsing.

This study was designed to contribute to the knowledge of lodgepole pine germination and to examine more closely within- and between-meadow variability in establishment of pine seedlings. Specific objectives were to determine the extent to which successful establishment is associated with: 1) availability of seeds and possible losses over the winter, 2) vegetative cover and soil water content, and 3) predation by rodents and birds.

STUDY AREA

Two meadows that had not been grazed recently by range cattle, one large and wet and the other small and dry, were studied in California's Yosemite National Park. These meadows are located at 2100 m near Glacier Point Road on the trail to Lost Bear Meadow (Fig. 1). Both meadows are surrounded by lodgepole pine stands, have vegetated rather than sandy margins, and are montane rather than subalpine. The larger site (3.37 ha) has topography of type A, formed in a basin; the smaller site (1.83 ha) is type C, formed along a permanent stream (Ratliff 1985). The larger meadow ranges from good to excellent condition, i.e., having no abnormal erosion and with herbage production near the climatic potential. The smaller meadow ranges from good to very poor condition. The poorest conditions occur near the stream channel, which is a continuous gully 1–2 m deep where erosion has lowered the water table.

Several study sites (areas that differ in species composition; Ratliff 1982) occur in each meadow. They represent different meadow series as defined by their hydrologic and vegetative classifications (Ratliff 1985).

METHODS

Study sites. In late summer of 1981, five sites (sites 1–5) on the large meadow and four (sites 6–9) on the small meadow were selected to represent different microenvironments that could influence the

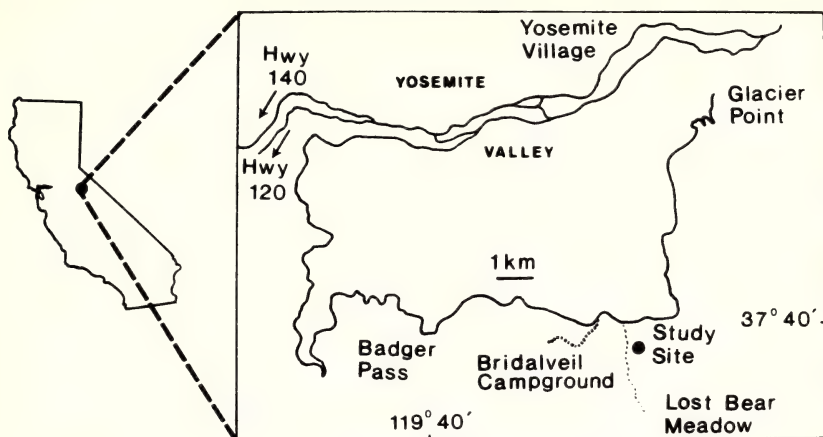


FIG. 1. Location of study.

success of lodgepole pine seedling establishment. Size and shape of sites varied with vegetation boundaries, but contained no less than 100 m². Because of small floristic differences, sites 2, 6, and 9 were subdivided for vegetation analysis. Rather than measure topography and microclimate directly, we evaluated site differences using floristic characteristics. This approach presumes that frequency and cover of particular herbaceous species are related to differences among microenvironments within the meadows, and that different species and their relative cover influence the capacity of lodgepole pine to invade meadows.

On each site, species frequencies were estimated using 100 randomly located 10 × 10 cm quadrats. Foliar cover (proportion of area under live aerial parts) and species composition were estimated at each seed plot. Site and species ordinations were derived from these data by reciprocal averaging (Hill 1973).

Soil characteristics near the center of each site were compared by taking a soil sample from the 10–20 cm depth. Samples were analyzed for: 1) percent sand, silt, and clay (estimated by the hydrometer method; Bouyoucos 1936); 2) percent organic matter [estimated by the loss on ignition method (ignition was for 4 hr at 600°C), Nelson and Sommers 1982]; 3) pH (estimated by the soil-water paste method with ionanalyzer; McLean 1982); and 4) bulk density at 0–10 cm and 10–20 cm depths [estimated by the cylinder (known volume) method, Cook and Stubbendieck 1986].

Soil depth to consolidated material was estimated using a probe, and depth to the water table was determined prior to fall precipitation in October 1983.

Seed plots. Ten replications of both uncovered and covered 0.1

m² plots containing approximately 50 seeds were established on each of the 12 sites in the fall of 1981 and again in the spring of 1982. Seeds were obtained from cones collected in 1981 from trees in an adjacent area. Seeds sown in the fall were unstratified. Spring sowing after snow melt utilized stratified seeds (soaked one day, held at 1.5°C in plastic bags for 28 days, sown wet; USDA 1974) to simulate the treatment that seeds receive as they overwinter on the meadows. Covers were made from 1.3-cm-mesh wire screen.

The number of seedlings in each plot was counted four times during the growing season in 1982, and also at the end of summer in both 1983 and 1984. Tests for significance of differences between mean survival at the end of three growing seasons were made using the Kruskal-Wallis non-parametric test for differences in means of ranked data grouped by single classification (Conover 1980). All plant nomenclature follows Munz (1959).

RESULTS

Vegetation

Twenty-three herbaceous species were found on both meadows; an additional 27 species occurred only on the large meadow and an additional 20 occurred only on the small meadow. Species with frequencies of 20% or more on at least two sites were used for vegetation analyses. The single axis reciprocal averaging ordinations of species frequency and composition data described similar arrays of herbaceous species on sites of decreasing moisture content. Consequently, species composition of the seed plots adequately defined the microenvironments of each site (Table 1).

Species most representative of wetter conditions (sites 4, 3, 5) were *Aster alpigenus*, *Carex nebraskensis*, *C. rostrata*, *Deschampsia caespitosa*, *Juncus orthophyllus*, and *Phalacroseris bolanderi* (Table 1). The moderately dry sites (sites 2, 6, 7, 1) were characterized by abundant *Aster occidentalis*, *Danthonia californica*, and *Trifolium longipes*. Species most representative of dry conditions (sites 8, 9) were *Horkelia fusca* subsp. *capitata*, *Lupinus confertus*, and *Penstemon rydbergii*.

Soils

Ordination of the sites from wettest to driest generally reflected increasing depths to the water table (Table 2). This shows a close relationship between species frequency, composition, and soil water availability. Also, with the gradient from wet to dry sites, organic matter decreased, and both bulk density (0–10 cm depth) and acidity increased. Soil textures and depths showed no apparent relationship to the moisture gradient.

TABLE 1. AVERAGE FOLIAR COVER AND SPECIES COMPOSITION OF SEED PLOTS AT 12 MEADOW SITES. Site ordination approximates a decreasing soil moisture gradient (left to right).

Characteristics	Wetter					Site							Drier		
	4	3	5	2b	2a	6b	6a	7	1	8	9a	9b			
	82.5	89.0	74.5	87.0	74.0	82.9	76.2	28.3	85.8	30.0	86.9	67.5			
Foliar cover (%)															
Composition (% foliar cover)															
<i>Phalacroseris bolanderi</i>	43.5	14.0	1.0												
<i>Carex rostrata</i>		5.0	6.0				0.6								
<i>Deschampsia caespitosa</i>		0.5	24.0	6.0											
<i>Carex nebraskensis</i>	3.5	11.0		6.5	5.5										
<i>Aster alpinus</i>	11.0	9.0	7.5	1.0	3.5				3.0						
<i>Juncus orthophyllus</i>	0.5	0.5	0.5						0.2						
<i>Eleocharis pauciflora</i>	32.0	41.5	4.5	34.0	24.0	25.0	35.6								
<i>Hypericum anagalloides</i>			1.0	4.5	1.0	0.4									
<i>Mimulus primuloides</i>	0.5		8.5	1.0						2.0					
<i>Juncus balticus</i>		0.5	0.5	5.0	0.5		1.9		0.5						
<i>Perideridia bolanderi</i>	3.5	4.0	5.5	2.5	6.5	3.3	7.5	1.9	0.8	0.5					
<i>Trifolium longipes</i>			0.5	0.5	11.5	18.8			5.2						
<i>Danthonia californica</i>			2.5	4.5	9.5	17.5	16.9	5.8	6.0	2.0					
<i>Muhlenbergia filiformis</i>	3.5	10.0	5.5	18.0	16.0	1.7		3.9	12.8	33.5					
<i>Aster occidentalis</i>			0.5	4.0	14.0	29.6	31.9	77.2	27.5	23.0	1.9				
<i>Stipa columbiana</i>								2.2	8.8	0.5					
<i>Agrostis idahoensis</i>							3.1	1.9		5.5					
<i>Pensstemon rydbergii</i>								6.9	3.0	14.8	10.0	7.0			
<i>Lupinus confertus</i>										4.2	10.0	6.0			
<i>Horkelia fusca</i> subsp. <i>capitata</i>									3.5		74.4	87.0			

TABLE 2. SOIL PHYSICAL CHARACTERISTICS OF 12 MEADOW SITES. Site ordination approximates a decreasing soil moisture gradient (left to right). SL = Sandy Loam; LS = Loamy Sand.

Characteristic	Site												
	Wetter						Drier						
	4	3	5	2b	2a	6b	6a	7	1	8	9a	9b	
Soil texture	54.3	69.0	71.3	73.9	80.5	65.4	67.3	69.3	80.6	59.8	63.4	67.4	
% sand	41.8	27.2	26.8	22.4	17.6	30.0	29.0	27.0	15.7	36.5	30.9	28.8	
% silt	3.9	3.8	1.9	3.7	1.9	4.7	3.7	3.7	3.7	3.7	5.6	3.7	
% clay	SL	SL	SL	LS	LS	SL	SL	SL	LS	SL	SL	SL	
Class	34.3	14.3	22.2	11.1	8.5	11.5	10.7	8.7	6.9	11.1	12.4	8.5	
Organic matter (%)	4.8	4.7	4.8	4.8	5.0	4.9	4.9	4.5	4.7	4.9	4.3	4.5	
Acidity (pH)													
Bulk density (g-cm ⁻³)	0.22	0.29	0.37	0.52	0.74	0.77	0.72	0.91	1.01	0.85	0.82	0.93	
0-10 cm depth	0.37	0.62	0.47	0.89	0.86	0.81	0.78	1.04	1.14	0.85	0.80	0.92	
10-20 cm depth	75	200	142	193	116	75	126	140	109	71	146	182	
Soil depth (cm)													
Water depth on													
7 October 1983 (cm)	2	6	12	7	20	50	47	58	40	78	84	72	

TABLE 3. THE NUMBER OF SURVIVING LODGEPOLE PINE SEEDLINGS PER SEED PLOT AT THE END OF THE THIRD GROWING SEASON AFTER SOWING 50 SOUND SEED PER PLOT. Site ordination corresponds to a decreasing soil moisture gradient (left to right) shown in Table 1.

	Site									Mean
	4	3	5	2	6	7	1	8	9	
Fall-sown: covered	0	0	0.4	5.6	3.1	29.5	0.0	10.7	0.1	5.48
uncovered	0	0	0	0.1	0.8	7.3	0.0	3.5	0	1.30
Spring-sown: covered	0	0	0	3.8	1.4	19.6	7.8	8.7	0.3	4.62
uncovered	0	0	0	0.7	1.7	11.2	2.1	3.5	0	2.13

Seed Plots

Fall seeding: covered seeds. On the large meadow, survival during the first year after sowing on sites 2, 4, and 5 was 20–30% and was substantially greater than the 2–4% survival on sites 1 and 3 (Fig. 2a). In the second year, survival on all sites except site 2 decreased rapidly. By year 3, survival on sites 1, 3, and 4 was zero (Table 3). On site 5, survival of 0.8% was lower ($p = 0.10$) than the 11.2% on site 2.

On the small meadow, seedling survival at the end of the first year was generally much higher (72.4, 48.8, 37.4, and 0%, respectively on sites 7, 8, 6, and 9). In subsequent years, survival decreased until by year three it was 59.0, 21.4, 6.2, and 0.2%, respectively. Mean survival on site 7 was significantly greater ($p = 0.05$) than on sites 8 and 6, and survival on site 8 was greater ($p = 0.10$) than on site 6.

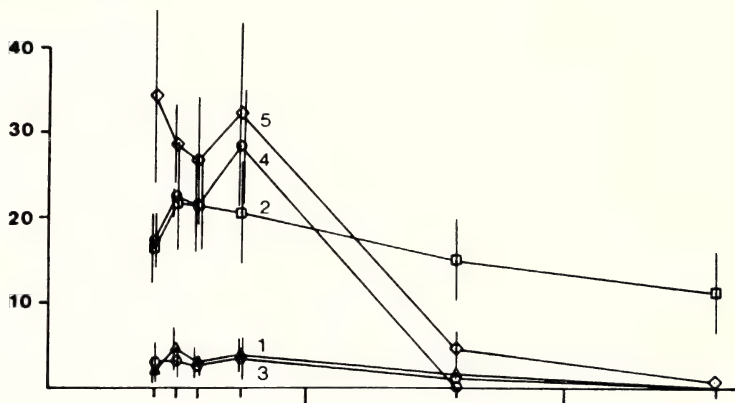
Fall seeding: uncovered seeds. On the large meadow at the end of the first year, survival was 28.0, 15.6, 4.0, 3.6, and 0%, respectively on sites 4, 5, 3, 2, and 1 (Fig. 3a). By the end of year two, survival on all sites had become close to zero.

On the small meadow, survival at the end of the first year was 28.0, 18.6, 7.8, and 0%, respectively on sites 6, 7, 8, and 9 (Fig. 3b). Mean survival on site 7 was greater ($p = 0.10$) than that on site 8; however, the means of survival on sites 6 and 7 were not different at that same level of significance. By the end of year three, survival was 14.6, 7.0, 1.6, and 0%, respectively on sites 7, 8, 6, and 9. This ranking of sites was the same as that on the covered seed plots.

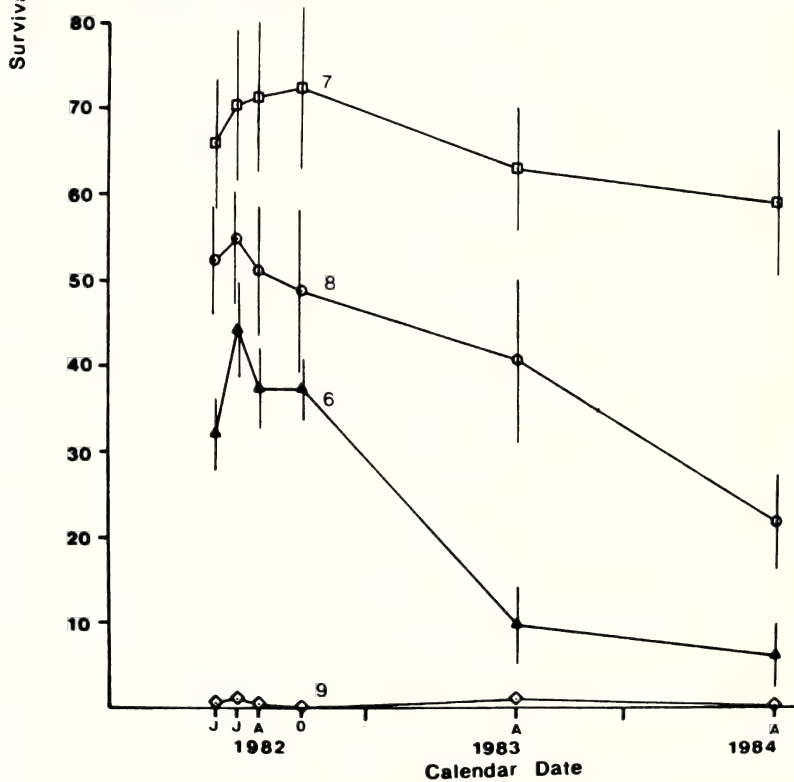
Spring seeding: covered seeds. On the large meadow, only sites 1 and 2 were sown because sites 3, 4, and 5 were under water until late summer. First-year survival on these two sites was 6.8 and 11.8%, respectively (Fig. 4). Second-year survival on site 1 increased to 28.1%, indicating additional germination of seeds on this driest site in the second year after sowing. At the end of year three, the

FALL SEEDING -- COVERED SEED PLOTS

a. Large Meadow



b. Small Meadow



mean survival on plots 1 and 2 was 15.6 and 7.6%, respectively, and these means were not different ($p = 0.10$).

On the small meadow, survival at the end of the first year was 47.4, 45.2, 25.4, and 0% on sites 8, 6, 7, and 9, respectively (Fig. 4b). Additional germination of seeds in the second year occurred on the driest sites 7 and 9. By the end of year three, survival was 38.2, 17.8, 2.8, and 0.7%, respectively in sites 7, 8, 6, and 9. Using $p = 0.10$ as a test of significance, the means of survival on sites 6 and 8, and on sites 7 and 8, were different, but means of survival on sites 6 and 9 were not.

Spring seeding: uncovered seeds. On the large meadow, the extent and pattern of survival were similar to those in the covered spots (Fig. 5a), but survival at the end of the third year was only 4.2% on site 1 and 1.4% on site 2, respectively; the difference between these means was not significant ($p = 0.10$).

On the small meadow, survival at the end of the first year on sites 6, 8, 7, and 9 was 18.0, 16.4, 14.0, and 0%, respectively (Fig. 5b). Sites 7 and 9 showed additional germination during the second year after sowing. By the end of year three, survival was 22.4, 7.0, 3.4, and 0% for plots 7, 8, 6, and 9, respectively. The difference between mean survival on sites 7 and 8 was significant ($p = 0.05$), whereas that between sites 6 and 8 was not.

DISCUSSION

Seed availability. Direct seeding of lodgepole pine showed that pine establishment in meadows is associated less with seed availability than with meadow type. On the wetter meadow, applying seeds in the fall to simulate natural seed fall showed that, despite abundant seeds, no seedlings survived through the second year (Fig. 3). On the drier meadow, up to 14% survival by the end of the third year indicates that invasion of this meadow type is much more likely (Fig. 3). Generally, for each meadow site, differences in survival between seeding in the fall and spring (Figs. 2 and 4; Figs. 3 and 5) were non-significant. This suggests that overwinter decreases in germinability and physical movement of seed off the site by melting snow are not important factors in the establishment of lodgepole pine.

Depredation. The similarity of pine seedling survival in covered

FIG. 2. Survival of lodgepole pine seedlings on fall-seeded, covered plots on sites 1-9 for the large and small meadows. Bars indicate standard errors of means; letters indicate months.

FALL SEEDING -- UNCOVERED SEED PLOTS

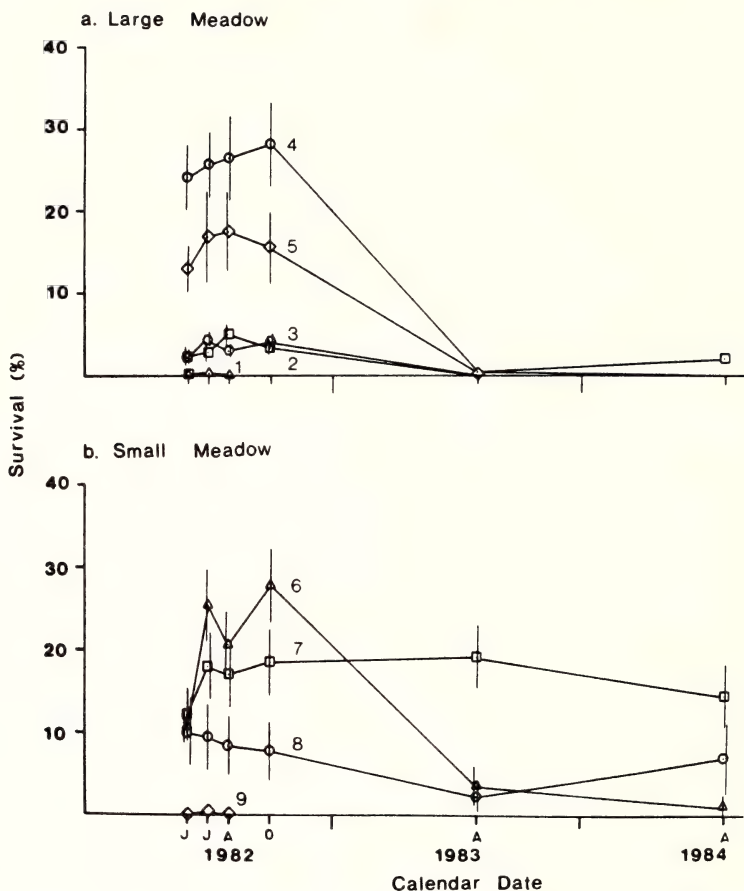


FIG. 3. Survival of lodgepole pine seedlings on fall-seeded, uncovered plots on sites 1-9 on the large and small meadows. Bars indicate standard errors of means; letters indicate months.

and uncovered fall-seeded plots on the large meadow (except for the drier site 2) (Figs. 2 and 3) suggests that depredation by rodents and birds on wet sites is unimportant. Covered, spring-seeded plots on the large meadow, however, had approximately twice the survival of the corresponding uncovered plots at each measurement date (Figs. 4 and 5).

Depredation was most apparent on the drier small meadow where germination and survival on uncovered fall-seeded plots were reduced by approximately 50% (Figs. 2 and 3). The effect of covering seeds and seedlings was less apparent on spring-seeded plots, with

SPRING SEEDING --COVERED SEED PLOTS

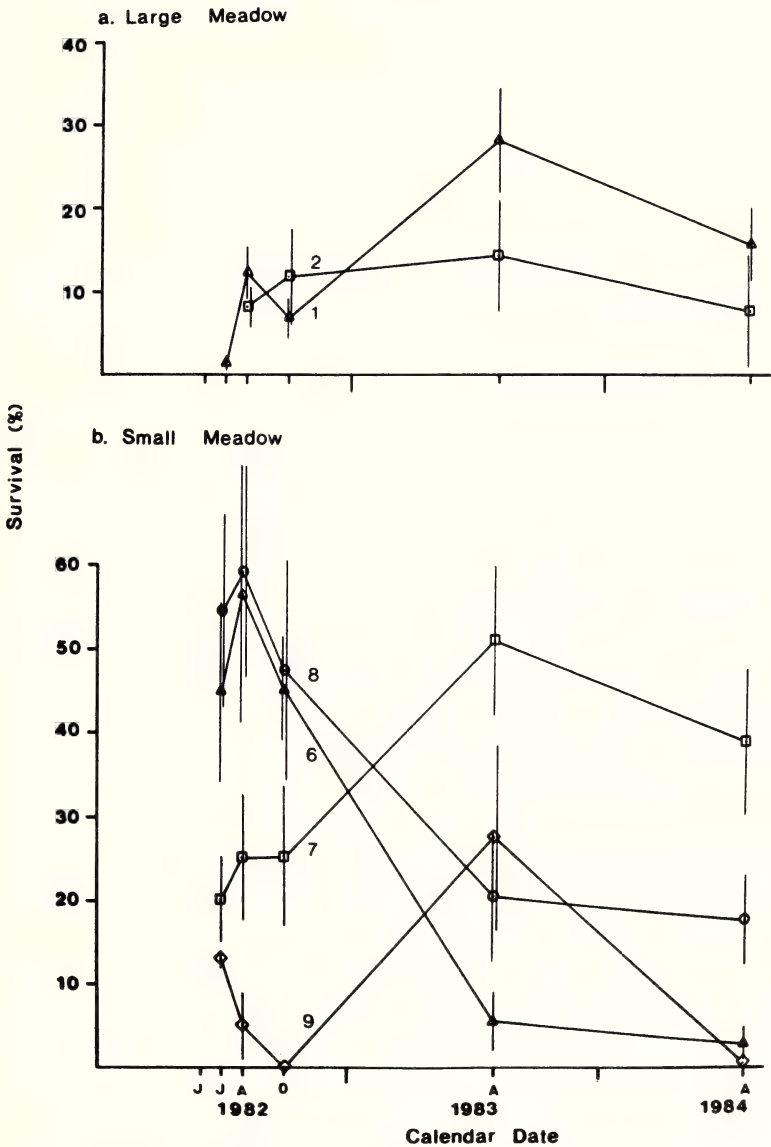


FIG. 4. Survival of lodgepole pine seedlings on spring-seeded, covered plots on sites 1-9 on the large and small meadows. Bars indicate standard errors of means; letters indicate months.

SPRING SEEDING -- UNCOVERED SEED PLOTS

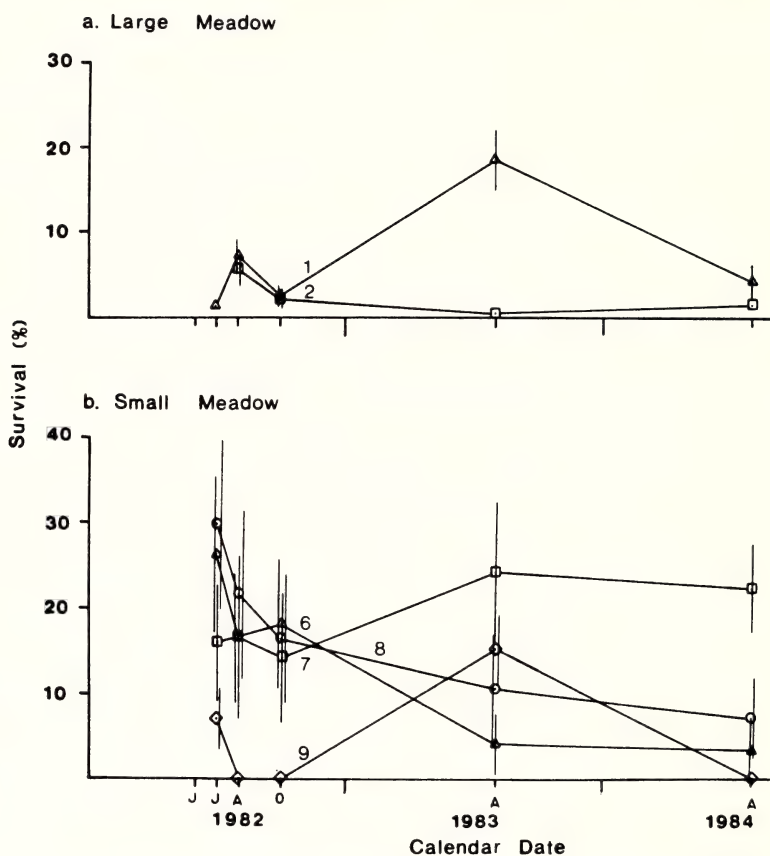


FIG. 5. Survival of lodgepole pine seedlings on spring-seeded, uncovered plots on sites 1-9 on the large and small meadows. Bars indicate standard errors of means; letters indicate months.

the notable exceptions of site 7 where seeds were sown on soil bare from gopher activity, and of site 8 that had only 30% foliar cover (Figs. 4 and 5). The greater survival of seedlings on the small meadow corresponds with its having a much larger number of previously-established outlier lodgepole pine trees.

Increased number of seedlings in the second year on the drier spring-seeded plots, 1, 7, and 9, may be associated with possible delayed germination of some seeds. This increase of approximately 8-25 seedlings per 0.1 m² plot probably is too large to be explained entirely by additional naturally-dispersed seeds. No new seedlings were observed adjacent to the plots.

Meadow type. Differences in frequency and cover of herbaceous species across meadows reflect differences in moisture regimes and potential for pine invasion. High potential occurs on moderately dry sites. These sites are usually too wet early in the year for much seed and seedling depredation. Later, these sites are not saturated but remain moist, which improves chances for establishment. Low potential occurs in the wettest and driest sites where either continuous saturation or moisture stress tends to prevent establishment.

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ANNOUNCEMENT

WOMEN BOTANISTS RECOUNT CAREER HARDSHIPS AND HIGHLIGHTS

Three women botanists describe the highlights of their careers as herbarium curators, collectors of native and ornamental plants, and conservationists of flora and habitat in this initial volume of a new series of oral histories on California Women in Botany. Produced by the University of California's Regional Oral History Office, the volume challenges the traditional view of botany as the pastime for the "weaker sex."

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INVASION OF *PINUS CONTORTA* VAR. *MURRAYANA* (PINACEAE) INTO MOUNTAIN MEADOWS AT YOSEMITE NATIONAL PARK, CALIFORNIA

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ABSTRACT

Stands of *Pinus contorta* var. *murrayana* (lodgepole pine) at the edge of many meadows have a tiered appearance due to bands of trees of increasing size class. Factors that might contribute to these waves of encroachment are seed availability and seedling establishment. Seed fall and distribution were monitored on two meadows in Yosemite National Park, California. Approximately 10,000–135,000 seeds/ha were distributed annually across the meadows. This probably represents 2–13% of seeds that fall commonly within lodgepole pine stands. First-year seedlings were estimated to be 550–10,000/ha annually. None of the naturally-established seedlings in the sample plots survived through the third growing season. Thus, waves of encroachment are more likely the result of success in establishment than of inadequate numbers of seeds or short dispersal distance. Nine 26–40 m transects from the meadow edge into the adjacent forest showed distinct periods of encroachment. On the wetter meadow these were 1950–1962 and 1918–1936. A comparison with records of precipitation available since 1907 shows that the two most recent periods of encroachment are associated broadly with periods of lesser precipitation. On the drier meadow, periods of encroachment were less distinct, but occurred during 1948–1973 and 1905–1931. Drier meadows are more conducive to pine establishment and encroachment is influenced less by patterns of precipitation.

Many mountain meadows in the Sierra Nevada, particularly the smaller, drier ones, are being invaded gradually by *Pinus contorta* var. *murrayana* (Grev. & Balf.) Engelm. (lodgepole pine) (DeBenedetti and Parsons 1979a). Invasion of meadows is a natural, dynamic process, but the factors that influence the rate of meadow invasion are not well understood. The phenomenon is of managerial and ecological interest. Conversion of meadows to stands of lodgepole pine reduces ecological diversity with adverse impacts on scenic, recreational, habitat, and grazing values.

Lodgepole pine in the Sierra Nevada is a prolific seed producer with crops of non-serotinous cones produced annually (Critchfield 1980). Seed fall in south-central Oregon has varied from 12,000 to over 2 million seeds/ha (Dahms and Barrett 1975). Although lodgepole pine has small seeds that are among the most dispersible of any North American conifers (Critchfield 1980), density of seedfall at a distance of 20 m from the timber edge may be only 10–30% of that within the stand, and most seeds fall to the ground within a distance of about 60 m (Lotan 1975, Lotan and Critchfield in press).

Invasion of lodgepole pine into meadows appears to be associated with warm-dry weather, grazing, and fire. The relative dryness of meadow soils is associated with the amount of snow and timing of snowmelt, which in turn are affected by the size and orientation of meadows (Anderson 1967). Similarly, Wood (1975) suggests that lodgepole pine seedlings tend to become established in years of low snowpack and that invasion patterns are affected by water table fluctuations. In the southern Sierran region, for example, changes in meadow vegetation are commonly associated with geological instability that in turn causes changes in water status (Benedict 1982). Vale (1981) concluded that although warm-dry weather is cited often as a major factor influencing lodgepole pine invasion into meadows, climatic fluctuations are typically less important than grazing or fire. Meadow disturbances from livestock grazing and trampling favors the establishment of pine seedlings, but also retards their development. Pines rapidly encroached into meadows when intensive sheep grazing ceased in 1900. Similarly, pine invasion into meadows of Kings Canyon National Park followed after the expiration of cattle grazing permits in the mid-1950's (Sharsmith 1959). Fire due to lightning strikes in grazed areas or due to the activities of Indians also influenced pine regeneration in meadows (DeBenedetti and Parsons 1979b).

I conducted this study to better understand the factors that influence the rate and timing of lodgepole pine invasion into meadows. My objectives were to determine 1) the dispersion of lodgepole pine seed into meadows from neighboring stands, 2) the extent of seed germination and establishment, and 3) the patterns of rate and timing of past lodgepole pine invasion into meadows.

METHODS

The large and small meadows selected for this study are located at 2100 m in Yosemite National Park, California, near Glacier Point Road on the trail to Lost Bear Meadow. They are the same meadows used for a concurrent study of lodgepole pine germination and establishment (Helms and Ratliff 1987). Detailed description of meadow physiography, soils, and vegetation are presented in that paper.

Natural seed dispersal. A sampling system of 195 and 95 seed traps was installed in the large and small meadows, respectively, in the fall of 1981, 1982, 1983, and 1984. They were in position from mid-August until snowfall was imminent in October. Traps were 0.1 m² in size, made of 2.5-mm-mesh wire screen, and positioned 1 m above the ground on a 10 × 10 m grid. The grids extended from the southern to the northern edge, and were located in the eastern half of each meadow.

TABLE 1. NUMBERS OF SEEDS/HA (\pm s.e.) DISTRIBUTED IN EACH MEADOW IN FOUR SUCCESSIVE YEARS.

Year	Large meadow	Small meadow
1981	28,830 \pm 6080	134,560 \pm 14,940
1982	23,240 \pm 4090	125,945 \pm 14,830
1983	9620 \pm 2850	24,760 \pm 6060
1984	20,861 \pm 8800	26,911 \pm 9300

Natural seedling establishment. A 0.1 m² plot was established 1 m north of each seed trap location. This provided a sample of 195 plots on the large meadow and 95 plots on the small meadow. Each fall, from 1982 through 1984, plots were examined for the presence of lodgepole pine seedlings.

Encroachment of lodgepole pine into meadows. Five transects were established in the large meadow and four in the small meadow. Each transect was 26–40 m long and extended from the meadow edge into the adjacent forest. Along each transect, 15–20 trees were measured in terms of height and distance from meadow edge. The age of each tree was determined by extracting a core from the stem at ground level and counting annual rings. Approximately 20 representative outlier trees within each meadow also were measured.

RESULTS

Natural seed dispersal. In each study year, a substantial cone crop was observed on the dominant trees with exposed crowns. Cone opening occurred on warm fall days. In the large meadow, the proportions of seed traps containing seeds in 1981, 1982, 1983, and 1984, were 17, 16, 6, and 23%, respectively. In the small meadow, the corresponding proportions in each year were 65, 88, 18, and 12%, respectively. The average annual seed fall on the large and small meadow over the four year period was 10,000–29,000 and 25,000–135,000 seeds/ha, respectively (Table 1). In the 80-m-wide small meadow, substantially more seeds were distributed within 30 m of the meadow edges than in the center of the meadow. This trend was not found in the large 220-m-wide meadow where the seeds were distributed more evenly.

Natural seedling establishment. In the large meadow, the total numbers of seedlings found in the 195 plots in 1982, 1983, and 1984 represent 550, zero, and 2200/ha, respectively. This is equivalent to two, zero, and 22% of seeds dispersed in the previous year (Table 1). On the small meadow, the total numbers of seedlings found in the 95 plots in the same years represent 4500, 4500, and 10,200/

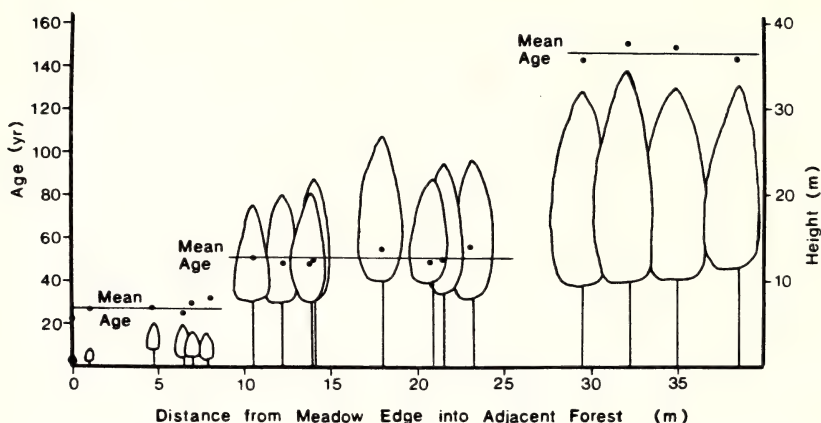


FIG. 1. Typical distribution of height- and age-classes in meadow-edge lodgepole pine of the large meadow.

ha, respectively, or 3%, 3%, and 41% of seeds dispersed in the previous year (Table 1).

In both meadows, the highest first-year survival occurred in 1984, which followed the smallest seed crop measured during the 4 yr study. All seedlings observed over the 3 yr of the study were ephemer-

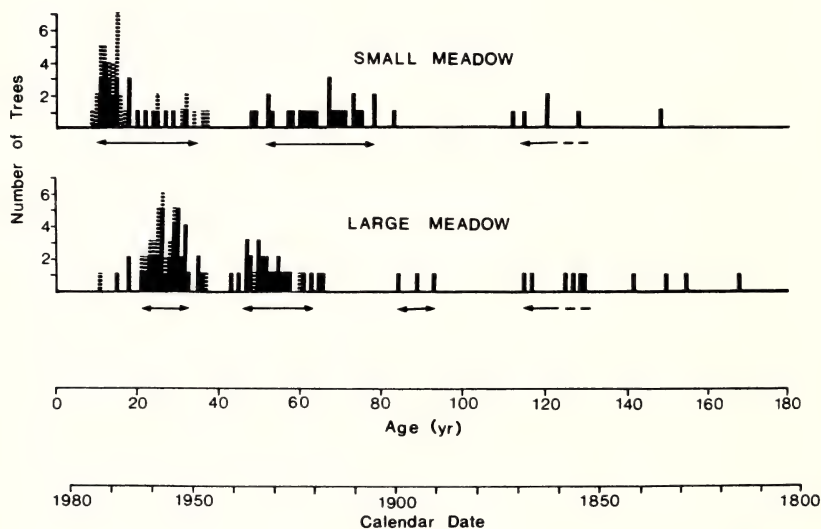


FIG. 2. Frequency distribution of age classes of meadow-edge trees (solid bars) from a total of nine 26–32 m transects, and all outlier lodgepole pine trees (hatched bars) in both the large and small meadows. Arrows indicate periods during which most encroachment of meadows occurred.

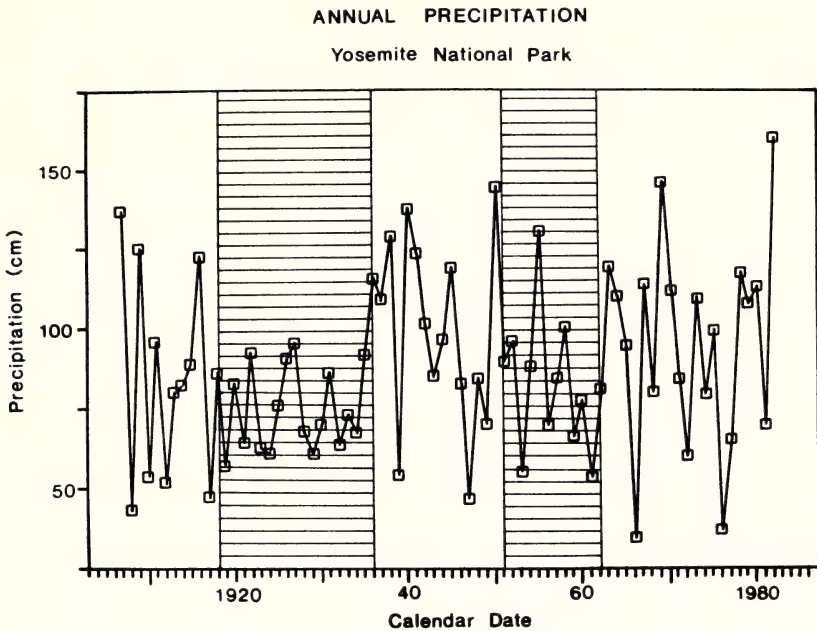


FIG. 3. Complete record of annual precipitation at the valley floor, Yosemite National Park, California. Hatched areas show periods during which most lodgepole pine encroached on the larger, wetter meadow.

eral. In only one case did a seedling survive into year two, but it did not survive through the third season.

Encroachment of lodgepole pine into meadows. The typical pattern of meadow-edge trees contained distinctly different age and height classes (Fig. 1). The large meadow was bordered by trees of two age classes: 21–33 and 47–65 yr and some older individuals that ranged from 80–170 yr (Fig. 2). These waves of encroachment occurred in the periods: 1950–1962 and 1918–1936, with older trees having become established prior to 1900. The small meadow was bordered by two, less distinct age classes: 10–35 and 50–80 yr and some older individuals that ranged from 115–150 yr. These age classes represent waves of encroachment occurring in 1948–1973 and 1905–1931, and some older trees established prior to 1860.

In the large meadow, two classes of outlier trees were identified: 1) 23.8 ± 1.3 yr and 6.02 ± 0.53 m in height, and 2) 49.0 ± 4.1 yr and 11.97 ± 0.79 m in height. These two classes correspond to the two youngest age classes of meadow-edge trees (Figs. 1 and 2). In the small meadow, the corresponding two classes were: 1) 13.6 ± 0.5 yr and 1.5 ± 0.13 m in height, and 2) 34.5 ± 1.1 yr and $12.68 \pm$

0.46 m in height. These two classes occur within the youngest age class of meadow-edge trees (Fig. 2).

No relationship was found between age of outlier tree and distance from the meadow edge. Outliers were located on slightly higher, drier locations within the meadows.

Correlation between encroachment and precipitation patterns. The periods during which most encroachment occurred on the larger, wetter meadow (Fig. 2) were superimposed on a complete record of annual precipitation (1907–1984) in Yosemite Valley (Fig. 3). Average precipitation during periods of no encroachment was 97.1 ± 5.4 cm. In comparison, average precipitation during periods of successful regeneration, was 80.5 ± 3.2 cm. The difference between these means was significant ($p \leq 0.02$). The smaller, drier meadow, in which channel erosion had lowered the water table, showed no apparent correlation between encroachment and precipitation.

DISCUSSION

Encroachment of pine seedlings into meadows was limited by lack of seedling survival rather than by inadequate seed supply or insufficient numbers of seedlings. In the large meadow, seeds distributed in the fall that escape predation may be washed away by free-flowing water that generally covers parts of the meadow until mid-summer. Invasion of lodgepole pine into meadows, therefore, is more likely at the meadow edge where there is higher seed fall and less flooding. The similar ages of both edge trees and outlier trees within the meadows suggests that conditions favorable for pine establishment in both locations occur concurrently.

The association between periods of most encroachment of lodgepole pine and periods of less precipitation (Fig. 3) is not strong, but provides support for the concept that invasion occurs under drier conditions.

In a study of lodgepole pine invasion near the Tioga Pass entrance to the park, the oldest tree found was established in 1866 (Vale 1981). Most trees were established from 1910–1975. No distinct pattern of invasion was found; however, most trees were established in 1925. Other periods reported to be associated with invasion are 1853–1875 and 1898–1909 (Boche 1974), 1910 (Vankat and Major 1978), and 1903, 1906, and 1924 (Wood 1975). Results of the present study suggest that variability in reported periods during which invasion occurred may be associated with wetness and size of meadow.

Rates of encroachment from 1868–present, determined by the relationship between age of trees and distance from the meadow edge, were 0.19 and 0.22 m yr⁻¹ for the large and small meadow,

respectively. At a similar rate of encroachment and with current meadow conditions the larger and smaller meadows will be invaded completely within ca. 580 and 180 yr, respectively.

ACKNOWLEDGMENTS

This study was supported by the USDA Forest Service, Pacific Southwest Forest and Range Experiment Station, Berkeley, California, Project Number PSW-80-0022. It also was part of the University of California's Agricultural Experiment Station Project 2942-MS. I thank Drs. W. Critchfield and F. Vasek for their helpful suggestions to improve the manuscript.

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THE DISTRIBUTION OF FOREST TREES IN NORTHERN BAJA CALIFORNIA, MEXICO

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ABSTRACT

This survey includes maps and provides descriptions of the distribution of 22 Pacific Coast temperate trees, including two endemics, in northern Baja California, from the international border south to latitude 30°. Ranges were discerned from aerial photographs and verified by field reconnaissance, botanical collections, and a low-altitude aerial flight. With the exception of mixed conifer and pinyon forests, most forests comprise single tree species that represent fragments of more diverse ecosystems from more mesic areas of California. The rapid decline in the diversity of Pacific Coast temperate trees below the international border reflects strong precipitation gradients associated with orography. Several California tree species have been reported erroneously in northern Baja California due to the misidentification of specimens, or the misinterpretation of common plant names or place names.

The southern geographic limits of many Pacific Coast temperate trees are in the mountains and coastal valleys of northern Baja California, Mexico. From various sources, Griffin and Critchfield (1976) mapped the ranges of these trees for California, but detailed maps stop at the international border. This survey includes detailed maps and provides descriptions of the natural distribution of 22 trees, including two endemics, in northern Baja California, from the international border south to latitude 30° (Fig. 1).

METHODS

Many localities are derived from botanical collections and field observations. Extensive collections, particularly by Wiggins (1980, DS), and Moran (SD) have probably recorded most of the flora of northern Baja California. I also consulted other botanical collections from SD, RSA, UCLA, and UCR. On each map I have plotted each collection that had definite locality data. Point records, however, are difficult to extrapolate into broader geographic distributions, because collections are invariably non-random and reflect particular interests and access. Indeed, many remote areas have never been visited.

Important locality data come from the extensive library of aerial photography at the Department of Earth Sciences, University of California, Riverside (Table 1). These photographs show the forests of northern Baja California, which are conspicuous in this semiarid shrubland landscape. I studied photographs on a Bausch and Lomb

TABLE 1. AERIAL PHOTOGRAPHS OF NORTHERN BAJA CALIFORNIA. ¹ = México 12, D.F.; ² = INEGI (Institute Nacional de Estadística, Geográfica y Informática), Mexico, D.F.

Source	Film	Year	Season	Scale	Resolution	Comments
Mexicana Aerofoto ¹	Black & White	1938	summer	1:20,000	good	lat. 31°45' to U.S. border
Mexicana Aerofoto ²	Black & White	1956	fall	1:40,000	good	comprehensive coverage south to lat. 30°
Mexico, INEGI ²	Black & White	1972	summer	1:50,000	excellent	comprehensive coverage

TABLE 2. AERIAL PHOTO CHARACTERISTICS OF TREES. Table data from Heller, Doverspike, and Aldrich (1964); map data for *Fraxinus velutina* var. *coriacea*, *Populus trichocarpa*, *Quercus engelmannii*, and *Q. wislizenii* based exclusively upon botanical collections. ¹ = Data only for species with diagnostic hues; other trees have nondistinct intermediate grey tones.

Species	Hue ¹	Adult height (m)	Height Crown spread (m)	Dis- tance crown base to ground (m)	Crown apex	Crown margins	Foliage	Comments
<i>Abies concolor</i>		20-30	4-8	<5	acute to narrowly rounded	serrate	dense	
<i>Calocedrus decurrens</i>	light	20-35	3-6	5-10	acute to narrowly rounded, broad base	entire to serrate	drooping	
<i>Cupressus arizonica</i>		2-10	1-3	0	acute	irregular adults	dense	even-aged stands
var. <i>stephensonii</i>	light	4-7	1-2	0	obtuse	irregular, ascending branches	juveniles spoked, dense	
<i>C. forbesii</i>						serrate	thin	even-aged stands
<i>C. montana</i>		10-15	1-2	<5	obtuse	serrate	frayed/thin	
<i>Pinus attenuata</i>		5-10	1-2	0	broadly rounded, straggling	irregular		
<i>P. contorta</i>		15-25	5-10	<5	acute to narrowly rounded	entire to serrate	thin	straight boles in shadows
<i>P. coulteri</i>		10-20	1-4	0-5	broadly rounded to obtuse	deeply serrate	moderately dense	branches rise at terminus

TABLE 2. CONTINUED.

Species	Hue ¹	Adult height (m)	Height Crown spread	Distance crown base to ground (m)	Crown apex	Crown margins	Foliage	Comments
<i>P. jeffreyi</i>		20-40	3-6	5-15	broadly rounded to flat	deeply serrate	moderately dense, columnar branches	
<i>P. lambertiana</i>		20-40	2-5	5-10	broadly rounded to flat	lobed	wheel spokes, stellate	branches pendulous
<i>P. monophylla</i>		10-15	1-2	0	broadly rounded to flat	sinuate ragged	frayed	
<i>P. muricata</i>		5-15	1-2	0	broadly rounded to flat	irregular	dense	even-aged stands
<i>P. quadrifolia</i>		10-15	1-2	0	rounded to conical	entire to slightly sinuate	moderately dense	
<i>Platanus racemosa-Populus fremontii</i>	dark	20-35	2-5	5-10	obtuse to acute	lobed sinuate	dense, limbs show	winter deciduous, gallery forest arrangement
<i>P. tremuloides</i>	light	5-20	3-6	<5	acute	entire to finely serrate	—	dense clone stand structure, winter deciduous
<i>Quercus agrifolia</i>	dark	10-25	1-2	3-5	flat	coarsely sinuate	dense	usually 2 or 3 primary spreading branches
<i>Q. chrysolepis</i> <i>Q. peninsularis</i>	dark light	5-10, 20 3-6, 15	0.5-1, 3 0.5-2	0 0-5	spherical flat	entire, slightly sinuate	compact moderately dense	partly winter deciduous, branches horizontal

roll film stereoscope with 3 and 8 \times magnification. Tree species were recognized from gross characters that included crown perimeter and shape, vertical structure, shadows, and color (hue) (Table 2).

Interpretation was verified by field reconnaissance and botanical collections. The process of developing diagnostic identification of trees required progressive cross-referencing between aerial photography and ground observations. Field data that were plotted on work maps or recorded on ground photographs also were correlated with aerial photographic signatures in the laboratory, and photographic information was verified in the field. I traveled through many forested areas of the Sierra Juárez, Sierra San Pedro Mártir, and several coastal sites (Minnich 1986). I flew one low-altitude reconnaissance (within 600 m of ground) in May 1986 from Tijuana to Cerro Bola, Valle Guadalupe, Cerro Los Pinos, Sierra San Pedro Mártir, Sierra Juárez, Valle las Palmas, and back to Tijuana.

Tree ranges were transferred from photographs onto 1:250,000 topographic quadrangles using a Bausch and Lomb Zoom Transfer Scope. The ranges shown on Figs. 2–16 will be modified by subsequent field research because the scale of aerial photography results in omissions, particularly local outposts and among species forming scattered small stands. Subtropical trees such as *Washington filifera* Lindl., *Erythea armata* Wats., and *Prosopis juliflora* (SW.) DC. are excluded from this treatment.

PHYSICAL SETTING

Physiography. The coastal valleys and mountains of northern Baja California extend into the southern part of the Mediterranean climatic zone along the Pacific Coast. Although the region is at the southern margin of reliable winter cyclonic storms, seasonally moist habitats are widespread because the large relief of mountainous terrain provides cooler temperatures with altitude and encourages orographic precipitation.

The physiography of the region can be subdivided into three ranges of the peninsular range province (Fig. 1) (Gastil et al. 1975). The Sierra Juárez, an extension of the Laguna Mountains of southern California, is an undissected plateau (elev. 1200–1800 m) of mostly granite substrate from the international border southeastward to near Santa Catarina. The southern third of the Sierra Juárez, south of Santa Catarina, is an extensive tableland of mesas capped by Miocene volcanics, with summits to nearly 2000 m.

Toward the Pacific coast, there is a discontinuous series of dissected, lower ranges (1000–1400 m), termed here the coastal Sierra Juárez, that extends southeastward from an unnamed range southwest of Valle las Palmas (Cerro Bola, 1280 m) to Ensenada Bay. Substrates include a granitic batholith, and extensive prebatholithic

(Cretaceous) undifferentiated volcanics, metavolcanics, and marine sediments (Alistos formation). The coastal and interior Sierra Juárez are separated by alluvial basins and low plateaus, including Valle las Palmas, Valle Guadalupe, Valle Ojos Negros, and an extensive high basin between Santa Catarina and El Alamo. South of Ensenada Bay, the coastal Sierra Juárez increases in altitude (1200–1500 m) and turns eastward along the Agua Blanca fault.

South of Valle la Trinidad, these transverse coastal ranges join the Sierra San Pedro Mártir batholith, characterized by a steep western scarp (vertical relief 700–1000 m) and extensive plateaus along the crest, the elevations of which decrease in steps from 2500 m in the north to 1800 m at Cerro Matomí. The area from the west scarp to the ocean contains extensive low foothills and mesas. These include a series of low northwest-southeast trending coastal ranges from Valle Santo Tomás to Colonet. The substrate is derived mostly from the Alistos formation, with Cretaceous marine sedimentary rocks (Rosario formation) outcropping along the coast. The faulted eastern scarps of the Sierra Juárez and Sierra San Pedro Mártir are rugged with numerous small canyons.

Climate. Annual precipitation results mostly from frontal storms that occur between December and March. It ranges from 200–300 mm in the coastal valleys to 500 mm in the mountains, and only 100 mm on lee slopes at the margin of the Sonoran Desert (Table 3). Heaviest precipitation occurs on the highest peaks of the coastal ranges, and on the western slopes of both the interior central Sierra Juárez and Sierra San Pedro Mártir. Despite their altitude, the southern Sierra Juárez tablelands are arid due to rainshadows created by the relatively high coastal peaks south of Ensenada. Because high relief becomes discontinuous along the peninsula south of the Sierra San Pedro Mártir, the rainfall, which is dependent primarily upon orography, becomes unreliable south of lat. 30°, where the Sonoran Desert extends west to the Pacific Coast.

Winters are mild from the coast inland to the interior valleys (Table 3). Ground inversions, however, produce cold nights and hard frosts in high mountain plateaus. Snowfall may account for no more than ca. 15% of the annual precipitation in the Sierra Juárez, but perhaps as much as 50% in the higher Sierra San Pedro Mártir (Minnich 1986a).

During summer, near-coastal valleys and western slopes of the coastal Sierra Juárez are cool, humid, and foggy because of the onshore flow of marine air with sea breezes and valley wind systems, as in California. Interior mountains and valleys are warm and dry except for occasional afternoon thundershowers that mostly occur along the eastern walls of the Sierra Juárez and Sierra San Pedro Mártir and are caused by surges of tropical moisture that move north along the Gulf of California from the subtropical Pacific Ocean.

TABLE 3. CLIMATOLOGICAL DATA FOR NORTHERN BAJA CALIFORNIA. (Mexico, no date). Data at stations with short records are normalized for long-term mean normals (1949-84), by 1° latitude bands at the following stations: lat. 32°, Presa Rodriguez, Valle Las Palmas, El Pinal; lat. 31°, Ensenada, Ojos Negros, Santo Tomás, San Vicente, El Alamo; lat. 30°, San Telmo, Las Escobas, El Rosario. ' = Estimate.

Station	Elev. m	Latitude/longitude (degrees & minutes)			Period of record	Temperature		Annual precip. cm
		°N	'	°W		Jan °C	Jul °C	
Near coast								
Planta Rosarito	22	32	18	117	1970-	13	20	24
Ensenada	24	31	52	116	1949-	13	20	26
San Telmo	70	30	58	116	1949-	11	21	20
Las Escobas	50	30	35	115	1949-	11	20	15
Coastal ranges & valleys								
Olivaros Mexicanos	351	32	03	116	1954-	12	23	32
San Carlos	170	31	47	116	1962-	13	21	30
San Vicente	110	31	20	116	1949-	12	22	22
El Rosario	82	30	04	115	1949-	14	22	15
Inland valleys								
Valle Las Palmas	280	32	22	116	1949-	12	25	20
Ojos Negros	712	31	55	116	1949-	12	25	24
Valle Trinidad	780	31	21	115	1968-	9	25	22
Rancho Santa Cruz	970	30	53	115	1959-	12	25	32
Mountains								
El Pinal	1350	32	11	116	1949-	8	22	44
San Juan de Dios	1275	32	07	116	1956-	7	22	41
Sierra Juárez	1580	32	00	115	1961-	5	19	36
Santa Catarina	1150	31	29	115	1958-	9	24	21
Parque Nacional								
San Pedro Mártir	2080	30	58	115	1981-	3	17	45 ¹

SPECIES DISTRIBUTIONS

The geographic distributions of northern Baja California trees reflect a number of factors, including altitudinal zonation, topography, substrate, and climatic gradients associated with orography, distance from the Pacific Coast, and latitude. With the exception of mixed conifer forests (*Pinus jeffreyi*, *P. lambertiana*, *Abies concolor*, *Calocedrus decurrens*) in the Sierra San Pedro Mártir and xeric pin-yons (*Pinus quadrifolia*, *P. monophylla*), most forests include single tree species with highly localized distributions that represent fragments of more diverse ecosystems in more mesic areas of California.

ABIES CONCOLOR (Gord. & Glend.) Lindl. (Fig. 2). White fir is common above 2200 m in the mixed conifer forest that covers the Sierra San Pedro Mártir. Individuals have been found as low as 1900 m along Arroyo los Pinos near Corral de Sam (Table 4). Although *Pinus jeffreyi* is the dominant tree of most forests in the range, *A. concolor* is locally dominant with *P. lambertiana* on steep northern exposures in the vicinity of Cerro Venado Blanco, Cerro la Botella Azul, and upper headwalls of the eastern escarpment, including Picacho del Diablo; a photo by Clyde (1975:85) records a sapling at the summit (3095 m). I have not seen *A. concolor* in extensive forests of *P. jeffreyi* south of La Grulla and La Encantada meadows. This tree has short, thick, wide leaves of the southern California-Rocky Mountain variety (Vasek 1985). The nearest stand is 180 km north in the Cuyamaca Mountains of San Diego Co., California (Griffin and Critchfield 1976), and, thus, is not known from the Sierra Juárez.

CALOCEDRUS DECURRENS (Torr.) Florin (Fig. 3). Incense cedar is rare even in the highest mountains of northern Baja California. In the Sierra San Pedro Mártir it grows mostly near streams from 1350–2400 m on the northern and eastern scarps of the plateau. It also has been collected along several arroyos to the south, as at La Corona, Valladares Creek, La Víbora, and La Encantada. The southernmost locality I have seen is along a gully 5 km south of La Grulla. Beyond stream habitats, incense cedar is occasional in mixed conifer forests at Vallecitos, including the largest tree of any species I have seen in the range (3 m dbh, 45 m height).

Moran found few *C. decurrens* groves in moist habitats within *Pinus jeffreyi* forest in the central Sierra Juárez, including La Matanza meadow, and Arroyo El Tule. Aerial photographs confirm his observation that the tree is relatively abundant along the canyon at El Tule. Federal foresters in Baja California have seen the tree along the arroyo that drains Laguna Juárez.

CUPRESSUS ARIZONICA Greene var. **STEPHENSONII** (C. B. Wolf) Beauchamp (Fig. 4). This variety of Arizona cypress was believed to be endemic to the Cuyamaca Mountains in San Diego Co. (Griffin and Critchfield 1976) until another larger cluster of populations was

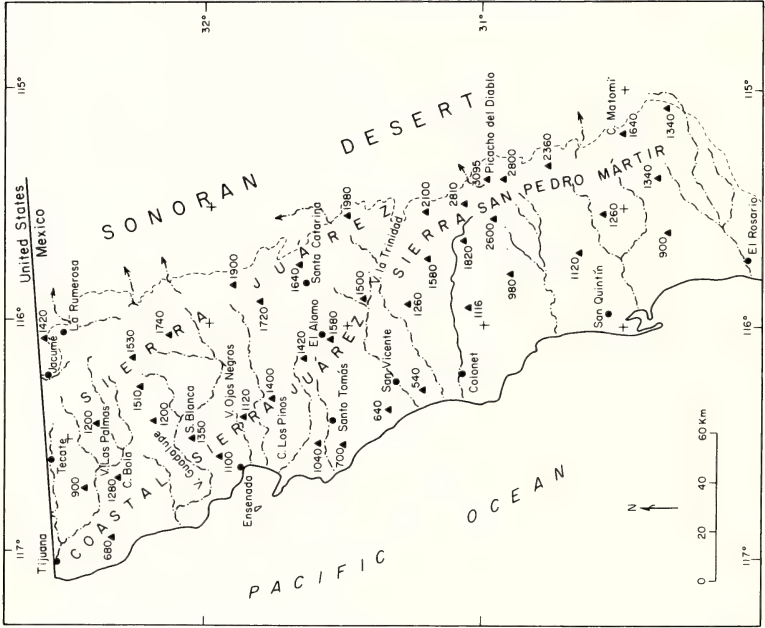


FIG. 1. Location map and place names of northern Baja California. Dashed line delimits Mediterranean vegetation (coastal sage scrub, chaparral, mixed conifer forest, pinyon forest) from the Sonoran Desert. ● = towns and villages. ▲ = mountain peaks.

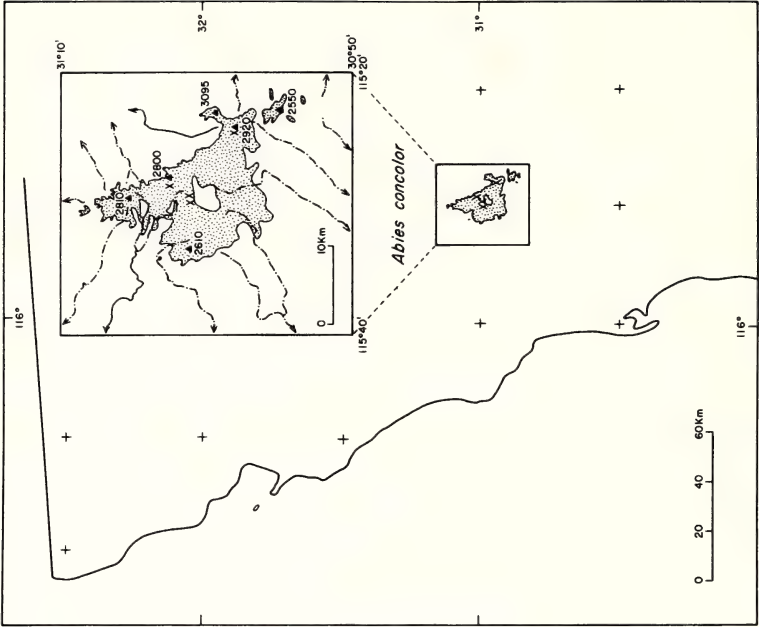


FIG. 2. The distribution of *Abies concolor*. Shaded areas mapped from aerial photographs. x = botanical collections.

discovered by Broder (1963) in the southern Sierra Juárez along Mesa Huicual, Mesa Valle Seco, and adjacent Cañada El Rincón southwest to near Santa Catarina (1200–1545 m). Trees along Cañada El Rincón are apparently old with large bole diameters (to 2 m), whereas stands on mesas are young due to chaparral fires (Moran 1972). A vaquero told Moran (pers. comm.) that the cypress also occurs in the next cañada south of El Rincón. In the 1986 aerial reconnaissance, I saw small colonies of this species to the southeast on an unnamed mesa south of Cañada El Rincón, on Mesa la Vinata Romero, in Cañón Alamito, and in Cañada la Esperanza. All stands grow on Miocene volcanics or Miocene postbatholithic continental sedimentary rocks (Gastil et al. 1975). Also, they occur in an area having a bimodal precipitation regime with limited winter rains, due to a rainshadow effect of the coastal Sierra Juárez, and with summer thundershowers. These conditions are similar to those of Arizona where *C. arizonica* occurs.

CUPRESSUS GUADALUPENSIS Wats. subsp. *FORBESII* (Jeps.) Beauchamp (Fig. 4). *Cupressus guadalupensis* subsp. *forbesii* occurs in San Diego County at Tecate Mountain, Otay Mountain, and near Guatay southwest of Cuyamaca Mountain (Griffin and Critchfield 1976). Botanical collections and aerial photographs show that these border populations are the northern limit of an extensive disjunct pattern of small groves. They are far more numerous than shown by Wolf (1948) and Little (1971) and occur for 150 km along coastal foothills of northern Baja California.

The northernmost stands in Mexico are extensions of U.S. populations at the border. Numerous colonies occur in near-coast foothills and mesas of the Cerro Bola range, especially at the south, between Cerro San Felipe and Cañada El Golpe. Interior outliers occur at Cerro Grande and 10 km south of Tecate. Another cluster of groves extends along the coast ranges north and east of Ensenada, from Rancho de la Cruz to Cerro Los Pinos, including Cerro Miracielo, Cañón los Cipreses, 1 km north of Cerro El Toro, and along the wash and adjacent northern exposures of Cañón San Carlos. To the south, isolated populations occur in coastal canyons with *Pinus muricata* west of San Vicente, above Rancho los Zaguaritos, an inland site at the summit of Cerro El Cipres (N), the upper headwaters of Cañón Nueva York, and at another Cerro El Cipres (S). Many groves are found at locations with “cipres” in place names on 1:50,000 scale topographic sheets.

Most stands grow in chaparral and are even-aged because of brushfires (see review by Vogl et al. 1977); scattered trees often occur in adjacent arroyos. The species grows between 200 and 1200 m, mostly on the Alistos or Rosario formations, although some inland and southern populations are on granodiorites. Nearly all stands grow on northern exposures, as in southern California (Vogl et al. 1977).

TABLE 4. PLACE NAMES¹ AND LOCATIONS. ¹ = Place names from 1:50,000 topographic sheets. ² = Specific locality of a collection or stand.

Place name	Latitude/longitude			Place name	Latitude/longitude		
	°N	'	°W		°N	'	°W
Agua Caliente de Guadalupe ²	30	38	115	Cerro Picacho la Vibora	30	52	115
Arroyo Barbón	32	00	116	Cerro San Felipe	32	04	116
Arroyo de Agua Amarga ²	30	23	115	Cerro San Luis ²	29	19	114
Arroyo El Cajón Jumpoff	30	53	115	Cerro San Matías	31	14	115
Arroyo El Huico	31	07	115	Cerro Venado Blanco	31	05	115
Arroyo El Ranchito	32	02	116	Cerro 2040 ²	30	40	115
Arroyo El Socorro ²	30	20	115	Cerro 2828	31	03	115
Arroyo El Taño ²	32	16	115	Corral De Sam	31	03	115
Arroyo El Tule ²	31	54	115	El Alacrón ²	31	52	115
Arroyo Hediondo ²	31	15	116	El Alamo	31	35	116
Arroyo los Pinos	31	04	115	El Topo	32	15	115
Arroyo Palizada ²	31	07	115	La Corona	30	58	115
Arroyo San Isidro ²	31	17	116	La Encantada	30	55	115
Arroyo San Antonio	30	48	115	La Grulla	30	55	115
Arroyo San Simón ²	30	38	115	La Matanza ²	32	04	115
Arroyo Santa Eulalia ²	30	38	115	La Rumerosa	32	30	116
Arroyo Santo Domingo ²	30	46	115	La Tasajera	30	58	115
Caballo Muerto	31	50	115	La Vibora	30	52	115
Cañada Doña Petra ²	31	56	116	Laguna Juárez (Hanson)	32	03	115
Cañada El Alamoso ²	30	41	115	Los Encinos ²	31	20	115
Cañada El Diablito ²	31	04	115	Meling Ranch	30	59	115
Cañada El Golpe	32	07	116	Mesa Barreal	30	45	115
Cañada El Piquillo ²	31	46	115	Mesa Huicual ²	31	42	115
Cañada El Rincón	31	41	115	Mesa la Vinata Romero ²	31	37	115
Cañada la Esperanza ²	31	35	115	Mesa Valle Seco ²	31	41	115
Cañón Agua Escondida	32	07	116	Mike's Sky Ranch	31	06	115

TABLE 4. CONTINUED.

Place name	Latitude/longitude			Place name	Latitude/longitude		
	°N	'	°W		°N	'	°W
Cañón Alamito ²	31	36	115	Mount Augusta ²	29	07	115
Cañón Arce ²	31	58	116	Neji	32	22	116
Cañón Borreguero	32	00	116	Oak Pasture	30	57	115
Cañón del Diablo	30	57	115	Observatory	31	02	115
Cañón Dolores	31	27	115	Picacho del Diablo	30	59	115
Cañón El Carmen ²	31	57	116	Punta San Isidro ²	31	20	116
Cañón El Carrizo ²	31	13	115	Rancho de la Cruz	31	58	116
Cañón Huatamote	30	45	115	Rancho los Zaguaritos ²	31	05	116
Cañón la Presa	32	25	116	Rancho San Faustino ²	32	13	116
Cañón la Providencia	30	57	115	Rancho San Pedro Mártir	31	03	115
Cañón los Cipreses ²	31	49	116	Rio San Antonio ²	30	48	115
Cañón Nueva York ²	30	37	115	Rio San Rafael	31	05	115
Cañón San Carlos	31	48	116	San Julio Canyon ²	27	30	113
Cañón Santa Cruz ²	31	26	116	San Pablo	31	30	115
Cerro Blanco ²	31	58	116	San Vicente	31	19	116
Cerro Bola	32	22	116	Santa Catarina	31	40	115
Cerro Chato ²	30	35	115	Santa Rosa Meadow	30	48	115
Cerro El Cipres (north) ²	31	27	115	Sierra Blanca	32	03	116
Cerro El Cipres (south) ²	30	23	115	Sierra San Borja ²	28	49	113
Cerro El Topo ²	32	13	116	Sierra San Luis ²	29	19	114
Cerro El Toro	31	53	116	Tecate	32	28	116
Cerro Grande ²	32	27	116	Uribes ²	30	19	115
Cerro la Botella Azul	30	58	115	Valladares ²	30	56	115
Cerro los Pinos	31	45	116	Vallecitos	31	00	115
Cerro Matami ²	30	22	115	Valle los Pinos	32	23	116
Cerro Miraciello	31	56	116	Valle Ojos Negros	31	50	116

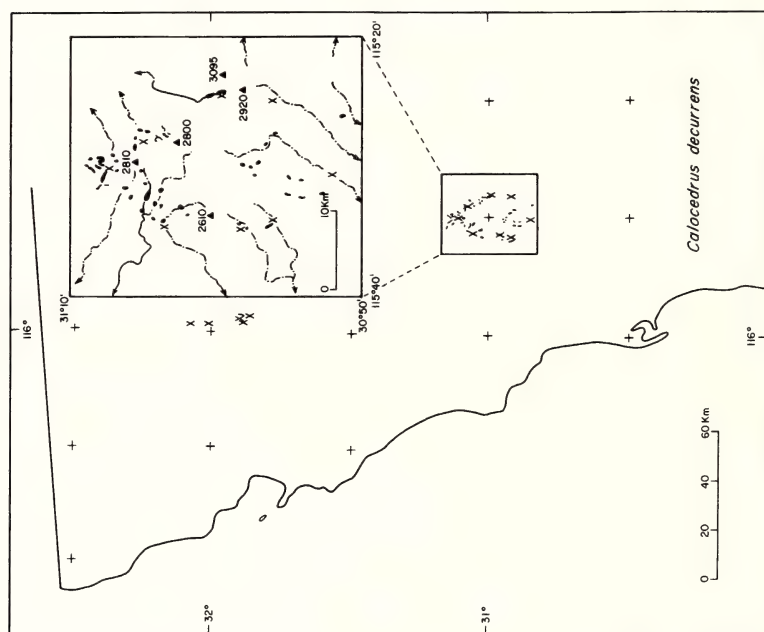


FIG. 3. The distribution of *Calocedrus decurrens*. Shaded areas mapped from aerial photographs. x = botanical collections.

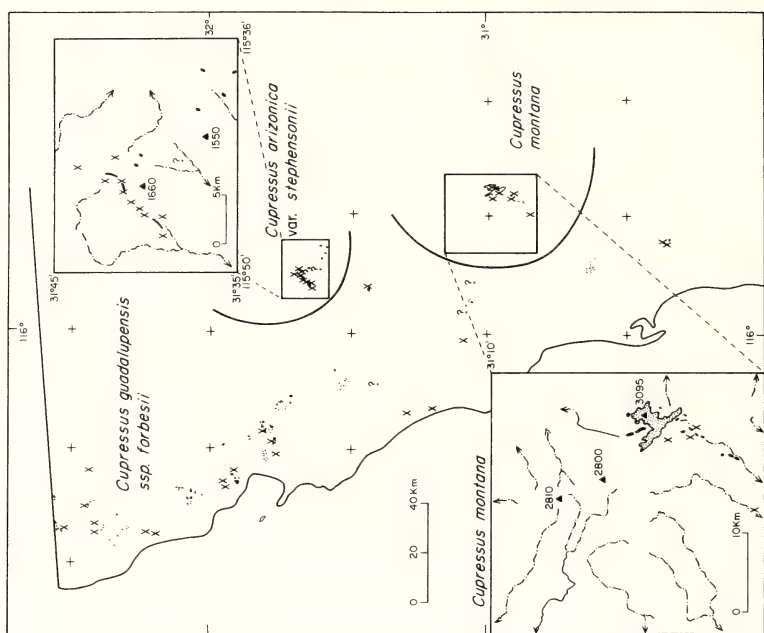


FIG. 4. The distributions of *Cupressus arizonica* var. *stephensonii*, *C. guadalupensis* subsp. *forbesii*, and *C. montana*. Shaded areas mapped from aerial photographs. x = botanical collections.

Cupressus guadalupensis also forms a significant forest on Guadalupe Island.

CUPRESSUS MONTANA Wigg. (Fig. 4). *Cupressus montana* is endemic to the Sierra San Pedro Mártir. Most stands are associated with a *Pinus lambertiana*-*Abies concolor* forest on steep granite walls along the eastern rim above 2200 m in the upper headwaters of Cañón del Diablo, Cañón la Providencia, and on the massive faces of Picacho del Diablo to near the summit (3095 m). Unlike many species of cypress, this tree develops great girth at the bole (1–2 m diam) and, thus, may be long-lived because forest productivity at these altitudes is diminished by cold climate. Juveniles may be seen down to 1400 m along Cañón del Diablo with *Quercus chrysolepis*, *Calocedrus decurrens*, and *Salix* spp. Scattered trees also are found along arroyos on the plateau, near Los Llanitos, above La Encantada, and on the main drainage between this meadow with La Grulla. Moran found one tree at La Vibora.

FRAXINUS VELUTINA Torr. var. CORIACEA (Wats.) Rehd. (Fig. 13). Arizona ash has been recorded in botanical collections in the southern Sierra San Pedro Mártir and adjacent coastal foothills, the Uribes, and along an unnamed arroyo near Cañada El Alamoso (800–1000 m). Wiggins collected the tree at Arroyo de Agua Amarga and at Agua Caliente de Guadalupe on the desert slope. *Fraxinus velutina* also occurs in San Julio Canyon in the Sierra San Francisco of central Baja California. The absence of records for Arizona ash in more mesic parts of the Sierra San Pedro Mártir and Sierra Juárez is peculiar. Several colonies in San Diego Co. at the international border (Griffin and Critchfield 1976) suggest that more intensive exploration will uncover other stands in northern Baja California.

PINUS ATTENUATA Lemmon (Fig. 5). Until recently, knobcone pine was collected only in the vicinity of Rancho de la Cruz, Cañón Arce, and Cañada Doña Petra (250–500 m) on the west flank of Cerro Miracielo (1100 m), north of Ensenada (cf. Map 58 in Critchfield and Little 1966). Aerial photographs from 1938 and 1956, however, show numerous stands along the north slope of this peak to near Cerro Blanco and Cañón Borreguero. Three groves were discovered by aerial reconnaissance 20 km southeast on a ridge at Cerro los Pinos. *Pinus attenuata* was recently collected in Cañón El Carmen, west of Valle Guadalupe. Occasional stands also may be present among numerous groves of *Cupressus guadalupensis* subsp. *forbesii* in the southern Cerro Bola range.

Similar to *C. guadalupensis* subsp. *forbesii*, *P. attenuata* grows in dense chaparral on the Alistos formation. Stands have an even-aged structure associated with canopy fires that are characteristic of the closed-cone pines (Vogl et al. 1977). Aerial photographs from 1972 show that most groves of *P. attenuata* on Cerro Miracielo were burned in a large fire in the late 1960's, but saplings were observed

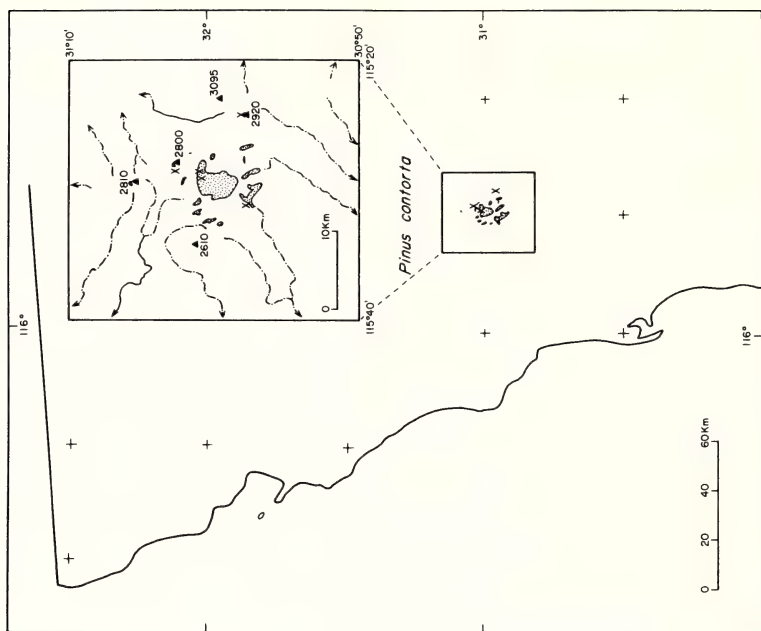


FIG. 6. The distribution of *Pinus contorta*. Shaded areas mapped from aerial photographs. x = botanical collections.

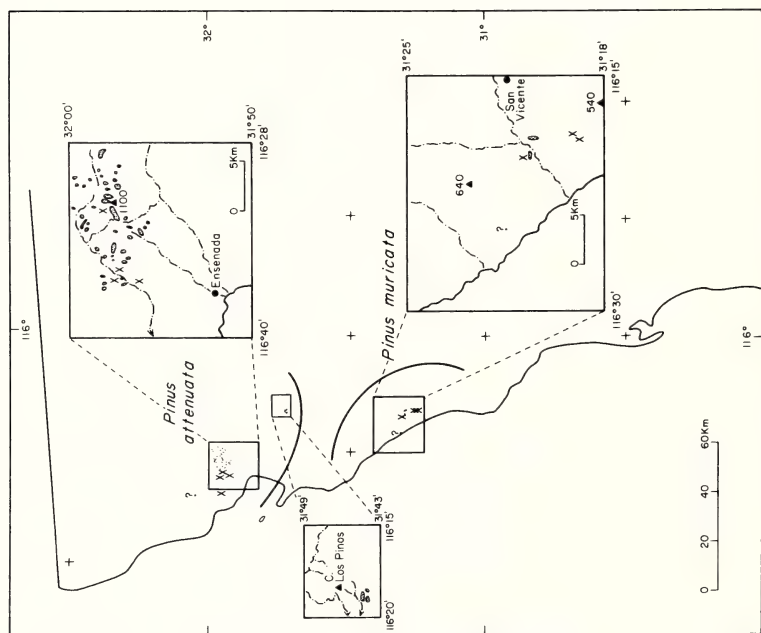


FIG. 5. The distributions of *Pinus attenuata* and *P. muricata*. Shaded areas mapped from aerial photographs. x = botanical collections.

throughout the burn in the 1986 aerial reconnaissance. The nearest stand in California is 200 km to the north, on Pleasants Peak in the Santa Ana Mountains (Griffin and Critchfield 1976).

PINUS CONTORTA Dougl. ex Loud. (Fig. 6). Lodgepole pine is confined mostly to the Vallecitos and La Tasajera basins in the Sierra San Pedro Mártir (2300–2400 m), where it typically becomes the dominant tree at edges of meadows. Smaller colonies descend adjacent arroyos. This subalpine forest tree is absent from mixed conifer forests covering higher ridges east of Vallecitos (2700–2900 m) except for scattered trees on northern exposures near the summits of Cerro la Botella Azul, Cerro “2828” (observatory), and Cerro Venado Blanco. A few individuals were reported recently from Picacho del Diablo at 3095 m (M. Hamilton, pers. comm.).

Characteristically, *P. contorta* prefers to grow on poorly drained sites where potential competitors cannot grow (Fowells 1965). Strong nocturnal ground inversions with temperatures as low as -15°C in winter and 0°C in summer (Alvarez 1981) also may permit this subalpine species to grow in basin floors. Its absence from the highest peaks may be due to rainshadow effects that extend from the wetter western rim of the plateau, where scattered populations are found along watercourses down to 2200 m. The nearest forest of *P. contorta* in California is in the San Jacinto Mountains (270 km north).

PINUS COULTERI D. Don (Fig. 7). Coulter pine is rare in northern Baja California (Minnich 1986b). Most colonies grow in mixed chaparral, often with *Quercus chrysolepis*, on highly resistant bedrock in mesic parts of the interior sierra. The only stand (100 ha) in the coastal Sierra Juárez is on Sierra Blanca (1250 m), southeast of Valle Guadalupe (cf. Griffin and Critchfield 1976). In the interior Sierra Juárez, isolated colonies grow on granites that occur southwest of Rancho San Faustino (1500 m) and hillsides immediately west and northwest of Laguna Juárez (1800 m). Aerial photographs indicate a number of small colonies in similar habitats between these localities. To the south, Moran (1977) found small populations at 1600 m on the Miocene volcanic tablelands on the north and south rims of Cañada El Rincón. Large colonies on the western margin of Mesa Huicual are clearly evident on aerial photographs. Moran (1972) stated that the cones in these populations were unusually small for the species, but did not mention whether there was evidence of hybridization with *P. jeffreyi*, which grows within 2 km in Arroyo El Rincón.

Several groves of *P. coulteri* were found by aerial reconnaissance in the Sierra San Pedro Mártir. Stands as large as 100 ha occur on northern exposures of the main divide immediately north of the plateau; another is on the headwaters of Arroyo la Palizada. In the southern part of the range, several stands are on the northeast and northwest flanks of Cerro “2040”. The San Pedro Mártir stands are

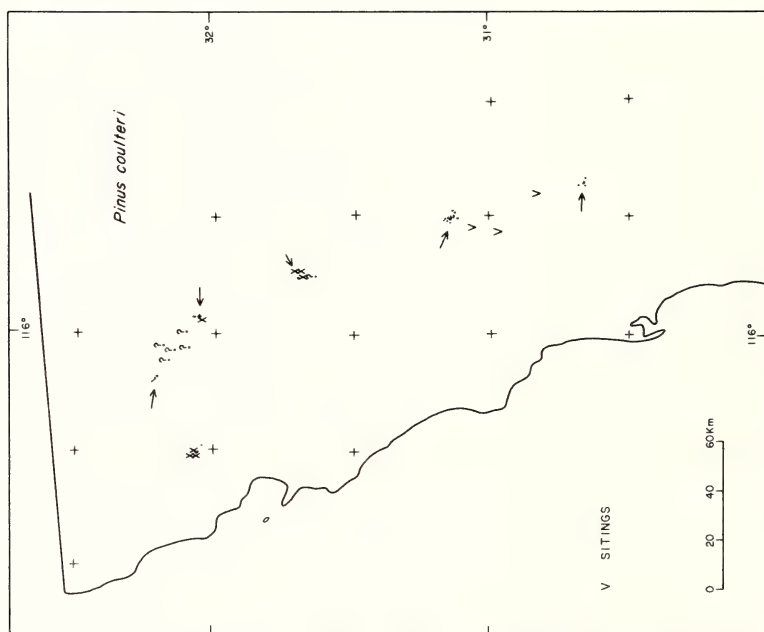


FIG. 7. The distribution of *Pinus coulteri*. Shaded areas mapped from aerial photographs. v = unverified sightings.

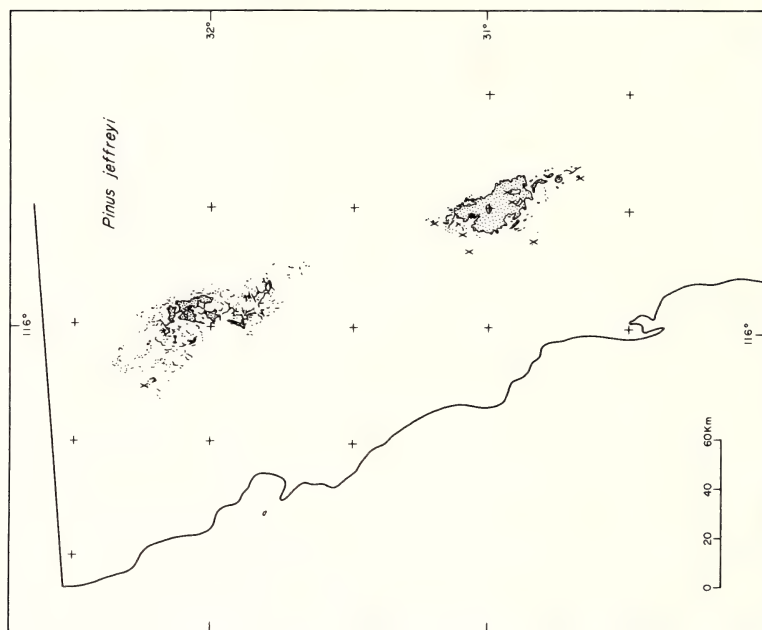


FIG. 8. The distribution of *Pinus jeffreyi*. Shaded areas mapped from aerial photographs. x = botanical collections.

all on northern exposures from 1900–2150 m. They also form even-aged stands that established after fires recorded on 1956 aerial photographs. According to Griffin and Critchfield (1976), three other *P. coulteri* localities occur in the range: northeast of Corral de Sam, upper La Corona Meadow (a single tree), and 8 km northwest of Santa Rosa Meadow. Although I have not seen any *P. coulteri* at these sites, Rojas-Gomez recently collected it at the northeast Corral de Sam site.

PINUS JEFFREYI Grev. & Balf. (Fig. 8). Jeffrey pine is the most important tree of mixed conifer forests along the crests of the Sierra Juárez and Sierra San Pedro Mártir (Minnich 1986b). Except for a few colonies of *C. decurrens* near watercourses, *P. jeffreyi* is the only tall tree in the Sierra Juárez, and forms extensive forests along meadows, basin floors, and watercourses above 1400 m from Valle Los Pinos to Arroyo El Rincón.

The northernmost stands in the Sierra San Pedro Mártir are five groves of ca. 50 trees on Cerro San Matías, an isolated peak (2100 m) 10 km north of the plateau. It recurs in several nearby basins (1600 m) in association with woodlands of *Quercus peninsularis* in the La Palizada, El Huico, and San Rafael drainages. On the Sierra San Pedro Mártir plateau above 2100 m, *P. jeffreyi* forms a zonal forest on slopes and basins above the chaparral belt in association with *Pinus lambertiana*, *Abies concolor*, *Quercus chrysolepis* and scattered understory of montane chaparral (*Arctostaphylos patula* Greene var. *platyphylla* Wells, *A. pungens* HBK., *A. pringlei* Parry, *A. peninsularis* Wells, *Ceanothus cordulatus* Kell., *Rhamnus californica* Esch., and *Quercus peninsularis*). It occurs up to 2900 m on the south face of Cerro Botella Azul. Scattered stands descend arroyos on the eastern scarp where it grows with *Calocedrus decurrens*. South of La Grulla and La Encantada meadows, *P. jeffreyi* again retreats to edges of meadows, basin floors, and arroyos down to ca. 1400 m. Moran found a few trees at 650 m near Río San Antonio on the west slope. The southernmost stands occur on Arroyos Fresnal and San Simón.

PINUS LAMBERTIANA Dougl. (Fig. 9). Sugar pine grows on the Vallecitos surface of the Sierra San Pedro Mártir, mostly on steep rocky slopes and cliffs in association with mixed conifer forest. It descends below elevations of *Abies concolor* (2100 m), with outposts extending further south beyond La Grulla and La Encantada meadows to Cerro Picacho la Víbora and scattered northern exposures near the Arroyo El Cajon jumpoff. A single tree at 1700 m was collected by Moran at Arroyo los Pinos near Rancho San Pedro Mártir. Sugar pine is locally dominant on the upper headwaters of the precipitous eastern rim and on Picacho Del Diablo up to 3000 m. The nearest stands in California are 200 km north, in the Cuyamaca Mountains of San Diego Co. (Griffin and Critchfield 1976).

PINUS MONOPHYLLA Torr. & Frém. (Fig. 10). Singleleaf pinyon grows almost exclusively along the arid eastern scarps of the Sierra Juárez and Sierra San Pedro Mártir. The geographic extent of *P. monophylla* was underestimated by Critchfield and Little (1966), who based their report on limited botanical collections.

In the Sierra Juárez, *P. monophylla* forms extensive forests above 1000 m in association with desert chaparral characteristic of the peninsular ranges (*Rhus ovata* Wats., *Quercus dununii* Kell., *Q. cornelius-mulleri* Nixon and Steele, *Rhamnus crocea* Nutt., *Yucca schidigera* Roezl ex Ortges., *Y. whipplei* Torr., *Juniperus californica* Carr.). A few pinyons cross the border at Jacumé into southeastern San Diego Co. A major forest with *P. quadrifolia* occurs on a large plateau surface from La Rumorosa to El Topo, with *P. quadrifolia* dominant on the wetter western margin and *P. monophylla* dominant on the eastern rim. In the wetter central Sierra Juárez, *P. monophylla* forests decrease to a narrow belt along the eastern scarp. Scattered colonies occur on both Pacific and desert flanks of the arid southern Sierra Juárez tablelands and northern foothills of the Sierra San Pedro Mártir adjacent to Valle la Trinidad.

Extensive forests with desert chaparral understory dominated by *Arctostaphylos peninsularis* and *Quercus peninsularis* are found on the eastern flank of the Sierra San Pedro Mártir from 1200–2000 m, above which it is gradually replaced by *P. quadrifolia*. As the elevation of the range decreases south of 30°50'N, *P. monophylla* decreases to scattered outposts on high ridges within the east scarp. It was collected on the north slope of Cerro Matomí. The southern limit of the species is near Cerro San Luis in north central Baja California.

PINUS MURICATA D. Don (Fig. 5). In northern Baja California, this closed-cone pine is known only from the foggy coastal foothills southwest of San Vicente, including Arroyo San Isidro (see Map 59, Critchfield and Little 1966), Arroyo Hediondo, and near Punta San Isidro. All stands grow in chamise chaparral or succulent coastal sage scrub (Mooney 1977) in the upper Cretaceous Rosario formation. A few colonies grow with *Cupressus guadalupensis* subsp. *forbesii*. *Pinus muricata* stands reported on Cedros Island (Critchfield and Little 1966) were recently named *P. radiata* D. Don var. *cedrocensis* (Howell) Axelrod (Axelrod 1980).

PINUS QUADRIFOLIA Parl. ex Sudw. (Fig. 11). Four-needled pinyon is the most widespread coniferous tree in northern Baja California, but rarely occurs below 1200 m. Over most of its range, *P. quadrifolia* forms scattered groves within relatively dense chaparral of *Adenostoma fasciculatum* H. & A. and *A. sparsifolium* Torr. on the mesic western flank of the interior Sierra Juárez or continuous forests with desert chaparral along the crest and east rim. *Pinus quadrifolia* is often allopatric with *P. monophylla*, which is confined to the arid

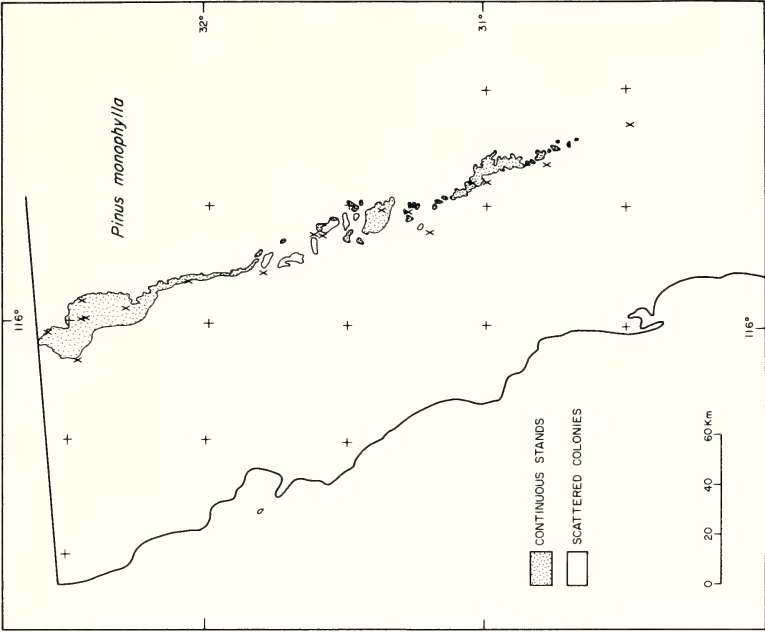


FIG. 10. The distribution of *Pinus monophylla*. Shaded and unshaded areas mapped from aerial photographs. x = botanical collections.

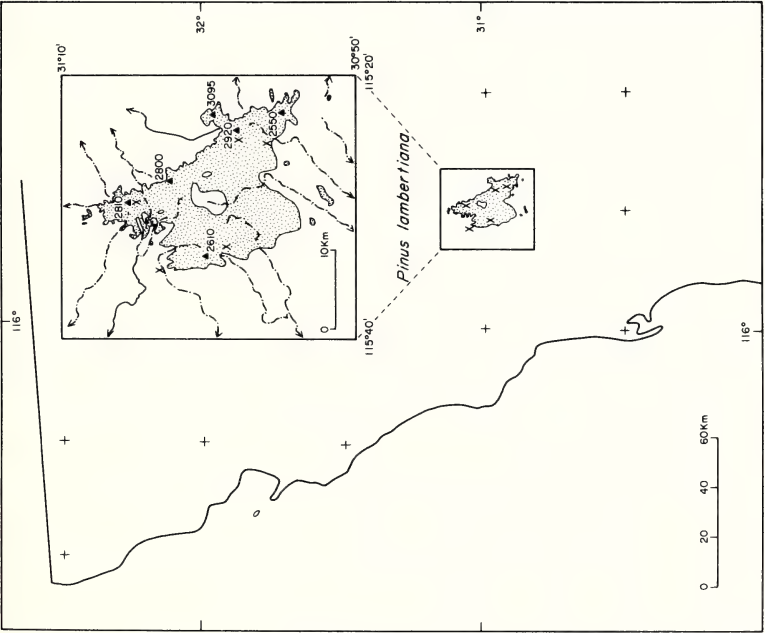


FIG. 9. The distribution of *Pinus lambertiana*. Shaded areas mapped from aerial photographs. x = botanical collections.

eastern scarps, similar to their distributions in the Peninsular Ranges of southern California (Map 16, Critchfield and Little 1966).

A few populations occur west of Jacumé near the international border. The most extensive forest overlaps with *P. monophylla* on the arid La Rumerosa-El Topo plateau, with smaller stands extending into shallow basins to the west. Numerous colonies pepper the chaparral belt on the Pacific slope of the wetter central Sierra Juárez, southward to Arroyo Barbón where the tree nearly drops out. The *P. quadrifolia* belt on desert drainages also narrows between the east margin of *P. jeffreyi* forests and *P. monophylla* forests on the eastern rim. *Pinus quadrifolia* then expands to form scattered cover on the Pacific and desert faces of the volcanic tablelands in the southern part of the range. Populations also extend westward along arid lee slopes on the coastal Sierra Juárez, including the Santa Catarina basin, El Alamo, and northwest to the southern edge of Valle Ojos Negros.

In the Sierra San Pedro Mártir, numerous groves of *P. quadrifolia* grow in mostly *Adenostoma* chaparral in higher basins north of the plateau. It then decreases to infrequent small colonies in dense chaparral on the mesic west flank of the range above the Meling Ranch. Stands become more frequent in the drier southern part of the range. Small outposts extend locally westward on higher spurs such as Mesa Barreal and major arroyos. On the eastern scarp, *P. quadrifolia* forms an extensive forest with *Arctostaphylos peninsularis*, *Quercus peninsularis*, and *Q. chrysolepis* understory from Cerro Venado Blanco to Arroyo El Cajon (1500–2500 m), where it meets Pacific slope groves. Although *P. quadrifolia* was collected up to 2700 m near the observatory, it is almost absent from the mixed conifer forest belt above 2100 m on the plateau. The southern limit is near Cerro Matomí.

Lanner (1974) provides evidence of extensive hybridization between *Pinus quadrifolia* and *P. monophylla* on the La Rumerosa-El Topo plateau. He suggests that *P. quadrifolia* should be replaced by *Pinus juarezensis* Lanner in this area.

PLATANUS RACEMOSA Nutt., POPULUS FREMONTII Wats. (Fig. 12). On aerial photographs, these riparian trees cannot be separated, but can be distinguished from other trees by their deciduous habit, canopy structure, and row-like stand arrangement along streams. Field reconnaissance indicates that most riparian forests consist primarily of *P. fremontii*.

The size of riparian forests is broadly proportional to streamflow. Stands are intermittent in the coastal Sierra Juárez where surface water is rarely permanent, except at Cañón Agua Escondida, and streams that cut through the ranges from the interior valleys. More continuous gallery forests follow the major arroyos descending the Pacific slope of the interior Sierra Juárez plateau below 1500 m,

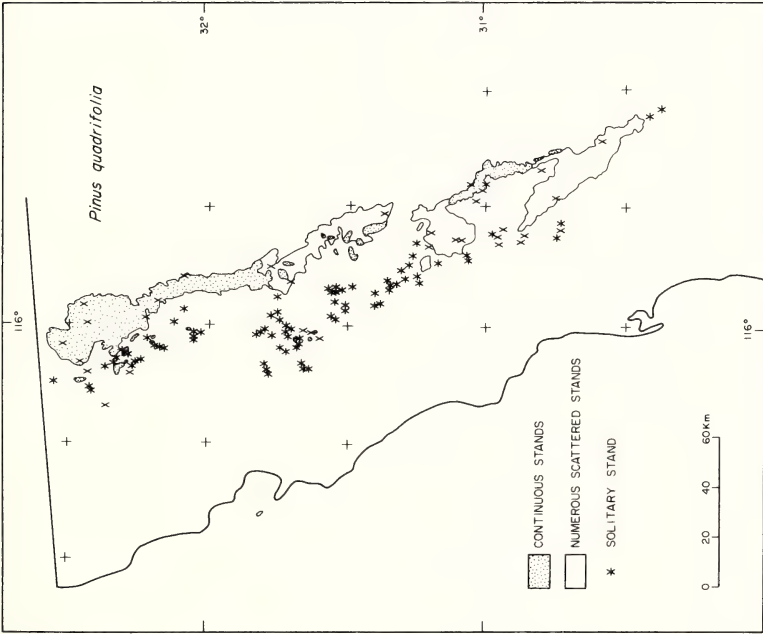


FIG. 11. The distribution of *Pinus quadrifolia*. Shaded and unshaded areas, and asterisks are mapped from aerial photographs. x = botanical collections.

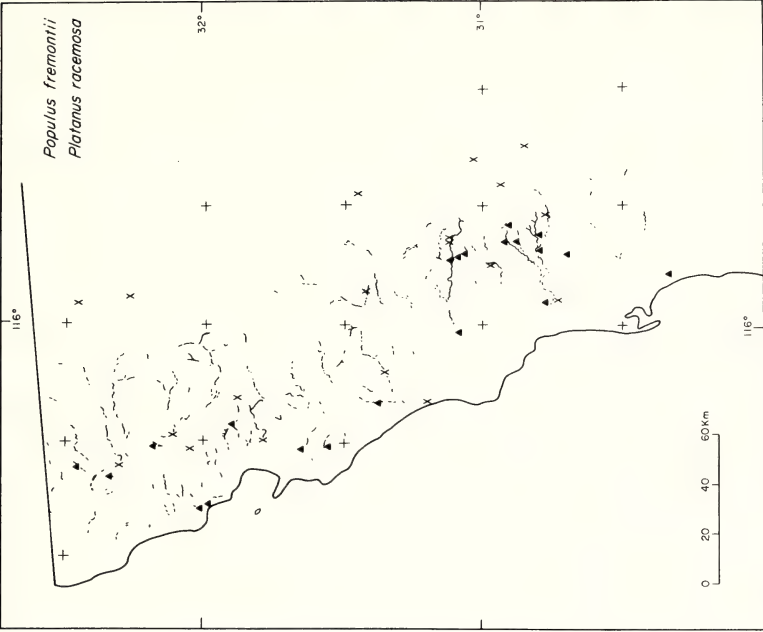


FIG. 12. The distributions of *Platanus racemosa* and *Populus fremontii*. Shaded areas are both species mapped together from aerial photographs. x = botanical collections of *P. fremontii*. Δ = botanical collections of *Platanus racemosa*.

except in the arid southern tablelands. The largest forests follow Arroyo Santo Domingo and Río San Rafael that drain the high Sierra San Pedro Mártir.

Botanical collections show that *P. fremontii*, the only tree to span the Baja California peninsula (Wiggins 1980), is occasional in desert canyons of both the Sierra Juárez and Sierra San Pedro Mártir, including Arroyo El Cajón, Cañada El Diablito, and Arroyo El Tajo. *Platanus racemosa* occurs mostly below 1000 m on the Pacific slope of the Sierra Juárez and western foothills of the Sierra San Pedro Mártir, and south to Arroyo El Socorro.

POPULUS TREMULOIDES Michx. (Fig. 13). Numerous groves of quaking aspen occur in the Sierra San Pedro Mártir above 2300 m along watercourses, on edges of meadows, and near springs. Most trees are small (<10 m), but some reach 25 m at permanent wet sites. Only the largest groves could be mapped and are recognized by their deciduous habit and compact grove structure on aerial photographs. These include stands near Cerro Venado Blanco, along the east ridge from the observatory to east of La Encantada Meadow, and margins of Vallecitos Meadow. On the eastern scarp, groves occur on the headwalls just northeast of the observatory and the upper north face of Picacho del Diablo. The nearest stands north of Baja California are two groves at Fish Creek and Gocke Valley, 350 km north in the eastern San Bernardino Mountains (Griffin and Critchfield 1976).

POPULUS TRICHOCARPA T. & G. (Fig. 13). Black cottonwood occurs at only two localities in the Sierra San Pedro Mártir: along Arroyo la Grulla (1400 m), 4 km southwest of La Grulla Meadow, and along Río San Rafael (1325 m).

QUERCUS AGRIFOLIA Neé (Fig. 14). Coast live oak, the most widespread hardwood tree in northern Baja California, grows mostly near stream banks, on meadow perimeters, and on basin floors within the chaparral belt. It occasionally grows on north exposures, especially near the international border.

Widespread stands in adjacent San Diego Co. (Griffin and Critchfield 1976) continue south along the mesic coastal flank of the interior Sierra Juárez below 1300 m. *Quercus agrifolia* is particularly abundant between Tecate and Nejí. Stand frequency decreases southward along the range except for large gallery forests along arroyos Barbón and El Ranchito. It drops out at Cañada El Piquillo, avoiding the arid southern Sierra Juárez tablelands. *Quercus agrifolia* is occasional in arid interior valleys north of Valle Ojos Negros.

In the coastal Sierra Juárez, *Q. agrifolia* is abundant in all the subranges from Cañón La Presa to Ensenada Bay and Valle Santo Tomás and continues southward along the near-coast foothills to Cañón Santa Cruz. At Valle Santo Tomás, scattered populations swing inland along the arroyos of the transverse coastal ranges par-

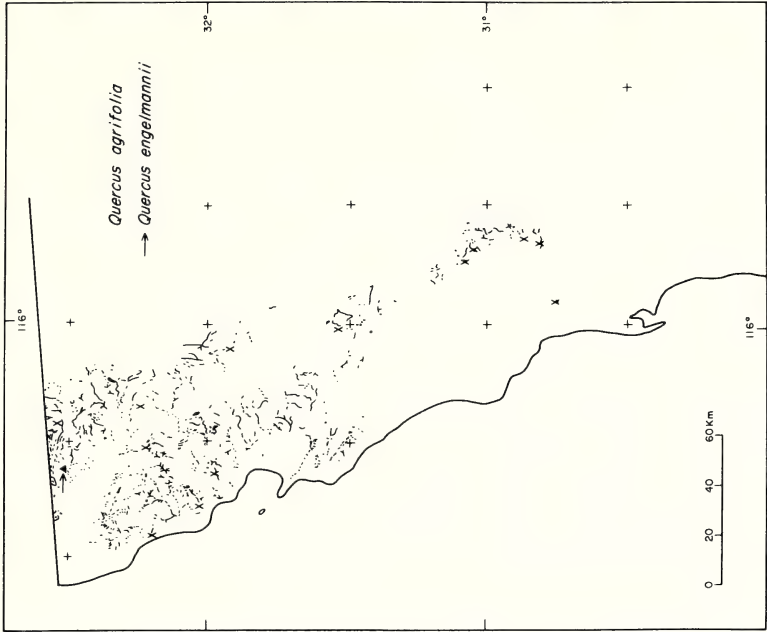


FIG. 14. The distributions of *Quercus agrifolia* and *Q. engelmannii*. Shaded areas are *Q. agrifolia* mapped from aerial photographs. Botanical collections: x = *Q. agrifolia*, Δ = *Q. engelmannii*.

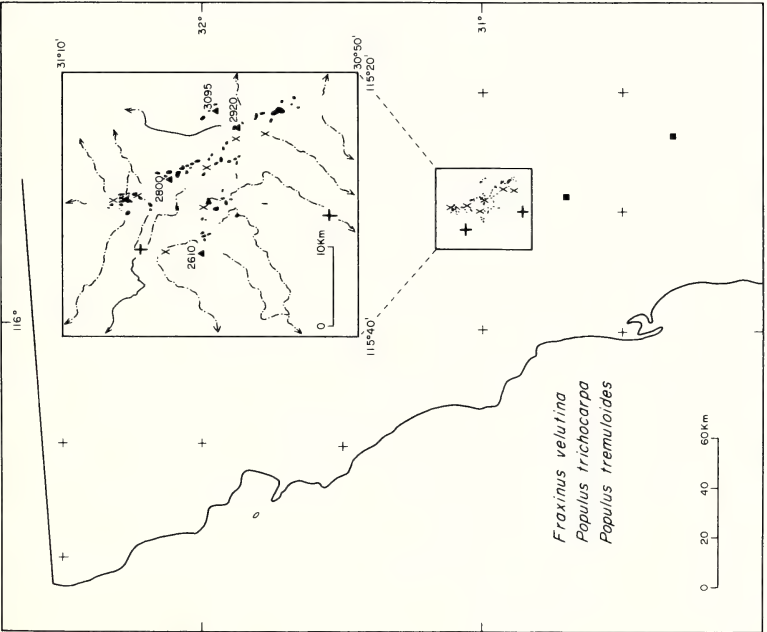


FIG. 13. The distributions of *Fraxinus velutina*, *Populus tremuloides*, and *P. trichocarpa*. Shaded areas are *P. tremuloides* mapped from aerial photographs. Botanical collections: x = *P. tremuloides*, + = *P. trichocarpa*, ■ = *F. velutina* var. *corticea*.

alleling the Agua Blanca fault to the east end of Cañón Dolores (cf. Orcutt 1887).

A single grove of *Q. agrifolia* at Los Encinos is the only population within a 25 km span between coastal Sierra Juárez forests and those at Cañón El Carrizo at the northwest end of the Sierra San Pedro Mártir. It is common along the major arroyos on the mesic western face of the high Sierra San Pedro Mártir from 1200–1700 m. The southernmost locality is a single grove on a stream bank near the coast along Arroyo Santo Domingo.

QUERCUS CHRYSOLEPIS Leibm. (Fig. 15). Most stands of *Quercus chrysolepis* consist of small-leaved shrubs to small trees (<8 m) (Myatt 1975) that grow on steep, well-drained slopes and canyons in the higher sierra above 1500 m. In the interior Sierra Juárez, *Q. chrysolepis* occurs mostly in chaparral on the highest peaks of the plateau. The largest stands concentrate around Rancho San Faustino, northwest of Laguna Juárez, near Caballo Muerto, and northern exposures of mesas and peaks in the southern tablelands. It is found at lower altitudes (1000–1400 m) on northern exposures of several peaks in the coastal Sierra Juárez (e.g., Cerro Bola, Sierra Blanca, and Cerro los Pinos).

In the Sierra San Pedro Mártir, outposts occur on Cerro San Matías (2100 m) and adjacent peaks at the north end of the range. A small grove of *Q. chrysolepis* is found on the north slope of Cerro Blanco (1900 m) near Mike's Sky Ranch. It is widespread in the highest part of the range above 1900 m, mostly as understory to *P. quadrifolia* forests on the east scarp and mixed conifer forests on the plateau, with scattered stands locally entering canyons and northern exposures at the upper margin of the chaparral belt on the west slope. It grows as a large tree (ca. 15 m) near streams along the headwaters of Arroyo la Palizada, and most deep canyons within the eastern scarp north of Picacho del Diablo that includes upper Cañón la Providencia. *Quercus chrysolepis* is absent from cold Vallecitos basin, and highest peaks above 2300–2700 m. South of La Grulla and La Encantada meadows, *Q. chrysolepis* is restricted to northern exposures of highest peaks. The southern limit is Cerro Chato.

QUERCUS ENGELMANNII Greene (Fig. 14). Although numerous populations of *Q. engelmannii* have been recorded near the international border in San Diego Co. (Griffin and Critchfield 1976), only a few trees have been found in northern Baja California (4 km south of Tecate). Although the partly winter-deciduous habit helps differentiate this tree from *Q. agrifolia*, aerial photographs in winter do not show recognizable populations elsewhere in Baja California. Scattered trees undoubtedly will be discovered at new localities, perhaps in the vicinity of Tecate and the Cerro Bola range.

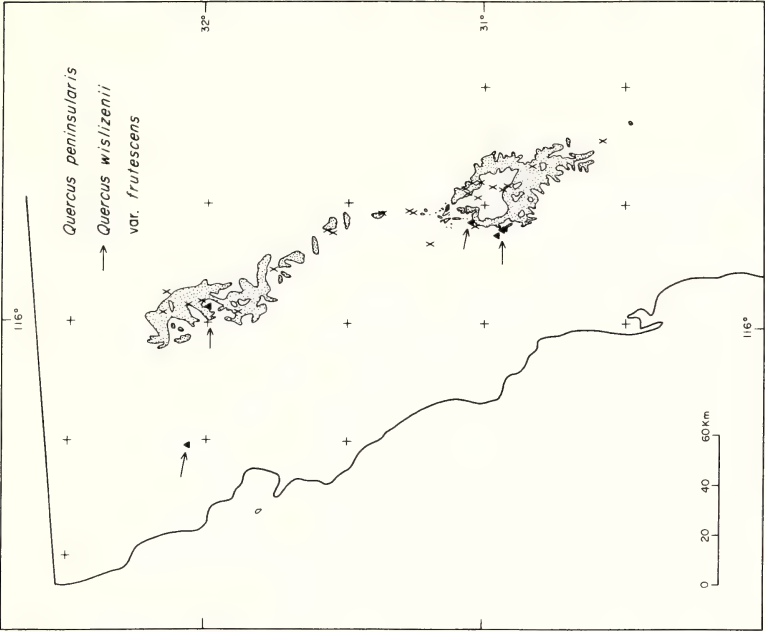


FIG. 16. The distributions of *Quercus peninsularis* and *Q. wislizenii*. Shaded areas are *Q. peninsularis* mapped from aerial photographs. Botanical collections: x = *Q. peninsularis*, Δ = *Q. wislizenii* var. *frutescens*.

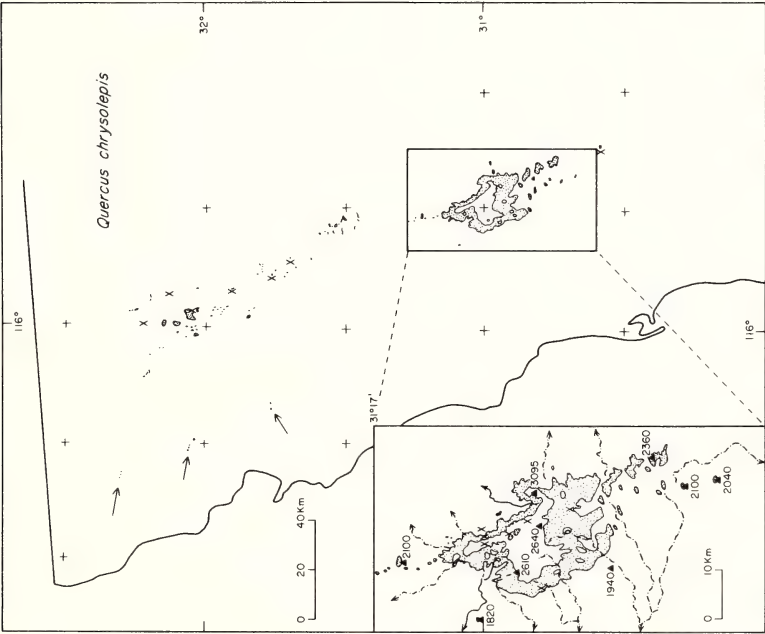


FIG. 15. The distribution of *Quercus chrysolepis*. Shaded areas mapped from aerial photographs, x = botanical collections.

QUERCUS PENINSULARIS Trel. (Fig. 16). An endemic to inland ranges of Baja California, *Q. peninsularis* is closely related to *Q. emoryi* (Muller 1965), widespread in northern Mexico, Arizona, and New Mexico. In the interior Sierra Juárez, *Q. peninsularis* is mostly a shrub to small tree in association with *P. jeffreyi* forests. The northernmost stand is near Cerro El Topo. It is occasional with pinyon forests along the east rim and the arid volcanic tablelands to the south. Botanical collections show that locally it descends arroyos on the Pacific slope down to 1200 m, avoiding the chaparral.

Quercus peninsularis is infrequent throughout the mixed conifer forest belt of the Sierra San Pedro Mártir; it is particularly abundant with *P. jeffreyi* forest at the south end of the range, where it occasionally grows into a robust tree 15 m in height and spread at wet sites. It is absent from the chaparral belt on the Pacific slope except along arroyos or forest margins. On the desert scarp, it is a zonal component of desert chaparral understory of *P. monophylla* and *P. quadrifolia* forests from 1000–2500 m from Cañada la Esperanza to Cañón Huatamote. Its abundance perhaps reflects summer rain on the eastern scarp, as in the area of *Q. emoryi* in mainland Mexico. The southernmost collection of *Q. peninsularis* in the Sierra San Pedro Mártir is from Cerro Chato. The tree occurs on the summits of Sierra San Luis, and Sierra San Borja, its southern limit.

QUERCUS WISLIZENII A. DC. var. *FRUTESCENS* Engelm. (Fig. 16). Field reconnaissances and botanical collections show that interior live oak is rare in northern Baja California and was not listed by Wiggins (1980). All known stands, usually a few individuals, occur at the conifer forest–chaparral ecotone (1200–1700 m) in the wettest parts of the Sierra. In the Sierra Juárez, it was seen or collected on Sierra Blanca and above Laguna Juárez. In the Sierra San Pedro Mártir, it was found on a steep northern exposure near Arroyo Los Pinos, at Arroyo La Corona, southeast of Oak Pasture, and in *Q. agrifolia* woodland below the Parque Nacional entrance. *Quercus wislizenii* is unusually large (to 10 m) at the latter site, confirming Brandegee's (1893) observation that it formed large bushes in the Sierra San Pedro Mártir. Further botanical collecting should expand the known range of this tree in northern Baja California.

OTHER SPECIES

Three tree species known primarily from California occur south of the border only in central Baja California. *Quercus tomentella* Engelm. occurs in an arroyo 3 km east of Mt. Augusta along the coast and on Guadalupe Island (Wiggins 1980); *Prunus lyonii* (Eastw.) Sarg. is found in the Sierra San Francisco northwest of San Ignacio. It appears that both trees survive at these localities in part through isolation from *Quercus chrysolepis* and *Prunus ilicifolia* (Nutt.) Walp.,

with which they freely hybridize (Muller 1965; Everett 1957). *Pinus radiata* D. Don grows in the summer stratus fog-drip zone of Cedros and Guadalupe Islands (700–900 m) (Critchfield and Little 1966).

NEAR MISSES

Several California trees have southern limits in the Cuyamaca Mountains within 50 km of the international border, including *Acer macrophyllum* Pursh, *A. negundo* L. subsp. *californicum* (T. & G.) Wesmael, *Alnus rhombifolia* Nutt., *Cornus nuttallii* Aud., *Pinus ponderosa* Dougl. ex P. & C. Lawson, *Quercus kelloggii* Newb., and *Umbellularia californica* (H. & A.) Nutt. (Griffin and Critchfield 1976). Although the biogeography of organisms seems to be influenced by the intensity of collecting and field surveys, the rapid decrease in forest diversity at the border may be no coincidence because of the strong precipitation gradients associated with relief. The Cuyamaca Mountains have a steep western face and no upwind rainshadows toward the Pacific Ocean. Precipitation from winter cyclonic storms concentrates along a narrow zone at the crest of the range, where annual amounts approach 1000 mm (California 1980). In the Sierra Juárez, orographic lift of rain-bearing air masses is spread over a wider area along gentle west-facing slopes. Rainshadows extend over the range from the coastal Sierra Juárez. Favorable orography on the steep west face of the Sierra San Pedro Mártir is compensated by decreased winter storm activity southward. Thus, few areas in northern Baja California have more than 500 mm annual precipitation, or half the amount in the Cuyamaca Mountains. In southern California, nearly all trees with southern limits in San Diego Co. grow in mesic habitats compared to trees with ranges extending into Baja California.

Several California trees have been erroneously reported in Baja California as a result of the misidentification of specimens and misinterpretation of common plant names and place names. Reports of *Pinus edulis* Engelm. in the Sierra Juárez and *P. cembroides* Zucc. in the southern Sierra San Pedro Mártir (Wiggins 1980) appear to be based on collections of *P. quadrifolia*. According to Moran, claims by rangers that *P. ponderosa* also occurs in the central Sierra Juárez are based on invalid taxonomic criteria (see also Duffield and Cumming, 1949; Wiggins, 1980). The only evidence for *Umbellularia californica* (cf. Wiggins 1980) appears to be a ranch named Tres Laureles, 5 km south of Tecate. References to *Pseudotsuga macrocarpa* (Vasey) Mayr in northern Baja California may have resulted from descriptions of “spruce” in the Sierra San Pedro Mártir or from confusion of a valley named San Felipe in Baja California with one in San Diego County (Minnich 1982). The reports of *Arbutus menziesii* Pursh (Wiggins 1980) are doubtful. Perhaps they are based on

18th century diaries by Arrillaga (Tiscareno 1969) and Longinos-Martínez (Simpson 1938) who use the name *madroño* in areas where *Arctostaphylos* spp. now occur, including hillsides above La Encantada (Longinos-Martínez), near San Pablo, west of Santa Catarina, ca. 5 km north of Valle La Trinidad, La Encantada, southern Valle San Rafael and several locations on the Sierra Juárez plateau (Arrillaga). Spanish diarists also may have confused the more rare *Heteromeles arbutifolia* with the Mediterranean *Arbutus unedo*, which is still called *madroño* in Spain. Likewise, references to "alder" (*Alnus rhombifolia*) by these diarists, as well as Serra (Tibesar 1955) and Crespi (Bolton 1927), appears to be a mistranslation for *Platanus racemosa*, which also was called "aliso". Thus, 18th century diarists probably saw sycamores when they traveled through northern Baja California.

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FIRE HISTORY OF AN OLD-GROWTH FOREST OF
SEQUOIA SEMPERVIRENS (TAXODIACEAE)
FOREST IN HUMBOLDT REDWOODS
STATE PARK, CALIFORNIA

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ABSTRACT

Establishment dates of basal sprouts of *Sequoia sempervirens* were found to be reliable estimates of known fires in Redwood National Park and Prairie Creek State Park in Humboldt Co., California. Fire history of an old-growth *S. sempervirens* forest in the Bull Creek watershed in Humboldt Redwoods State Park, northwestern California, was determined by analyzing *S. sempervirens* basal sprouts, fire scars, and dates of establishment of *Pseudotsuga menziesii* and *Abies grandis*. Fire frequency was estimated for watershed zones, for a clearcut area having fire scars, and for the entire study area. Conservative and liberal estimates of the fire cycle were made. Pre-settlement fire intervals were: 24.6 yr for watershed zones, 31 yr for the area with fire scars, and 13.3 yr for the entire study area. The conservative estimate of the fire cycle was 51.6 yr and the liberal estimate was 26.2 yr. Settlement fire intervals were: 15.6 yr for watershed zones and 7.5 yr for the entire study area. The conservative and liberal estimates of the fire cycle were 16 and 10 yr. Post-settlement fire intervals were: 7.8 yr for the watershed zones, 14 yr for the area with fire scars, and 4.5 yr for the entire study area. The conservative and liberal estimates of the fire cycle were 16 yr and 9.5 yr. Statistically significant differences ($p < 0.05$) were found between the fire interval means for all three settlement periods. No statistically significant differences ($p > 0.05$) were found between settlement period and fire size. Fire size was not correlated with fire frequency.

Throughout the 800 km range of *Sequoia sempervirens* there is abundant evidence of fire. In nearly all groves, trees exhibit fire scars, hollowed-out bases (goose pens), and/or bark char that extend many meters up the bole. The role of fire in *S. sempervirens* has been discussed (Fisher 1903, Fritz 1931, Stone 1966, Veirs 1982). One approach to deduce fire's natural role has been to determine fire history by aging fire scars on stumps. Near the southern end of the range of *S. sempervirens*, mean fire intervals of approximately 50 years (Greenlee 1983), and 22–27 yr (Jacobs et al. 1985) have been reported. Fire intervals near the northern end of the range have been reported to vary from 50–500 yr, that increase along a continuously mesic east to west gradient (Veirs 1982). Fritz (1931) concluded that on a 12 ha area, to the east of Weott, California, there was an average of 4 major fires per century over the past 1100 yr.

These studies provided good estimates of historic fire frequency, but did not establish exact calendar dates for fires and did not in-

dicating what size the fires may have attained. The determination of exact calendar dates is difficult because of 1) weathering of the outer rind of sapwood on old *S. sempervirens* stumps that obliterates the most recent annual rings, 2) the difficulty in determining when trees were cut, and 3) the production of discontinuous rings or absence of rings at stump height for large trees during drought or stress periods (Fritz 1931, LaMarche and Wallace 1972). An alternate method of determining fire frequency is to date *S. sempervirens* basal sprouts that presumably developed following fire. By using basal sprouts, the first two problems are eliminated and the latter problem would be minimized because the sprouts would be younger, more vigorous trees. Therefore, they would be less likely to have discontinuous or missing rings (LaMarche and Wallace 1972). Missing rings, however, are possible on young, vigorous sprouts if adjacent sprouts have grown together. Fritz (in Douglass 1928) observed that the interior radii of joined stump sprouts had fewer annual rings than did the exterior radii or those radii above the junction of the sprouts. This phenomenon can be avoided by sampling solitary sprouts. Lack of certainty that a sprout developed following fire is another possible problem in using basal sprouts as an indicator of historic fires. Although it has been well established that *S. sempervirens* sprouts following fire (Fritz 1931, Wiant and Powers 1967, Daubenmire 1975, and many others), it also sprouts following mechanical injury to its base (Fisher 1903, Wiant and Powers 1967, Lindquist 1979, and many others). When there is a ring of basal sprouts around a fire-damaged old-growth parent tree, it can be assumed that the sprouts developed because of fire.

The present study was undertaken to 1) verify that basal sprouts can be used to determine fire frequency; 2) determine the historic fire frequency in an old-growth *S. sempervirens* forest by dating basal sprouts and fire scars on stumps of *S. sempervirens*, and by dating other conifer species (*Pseudotsuga menziesii* and *Abies grandis*), and 3) estimate the area burned by each fire so that a fire cycle can be calculated.

FIRE RECORDS

Pre-1940 agency fire records are poor (Wallis et al. 1963). Archival fire records of the California Department of Forestry are incomplete for the 1920's and 1930's and for some years no records exist. There are no pre-1920 fire records on file. Gripp (1976) reviewed extensively the northwestern California newspapers and various other documents and found that large fires in Humboldt and Del Norte cos. were common. He concluded that between 1880-1939 the mean interval between severe fire seasons was 3.3 ± 0.79 (s.e.) yr.

In a study of large fires occurring in Humboldt and Del Norte cos.

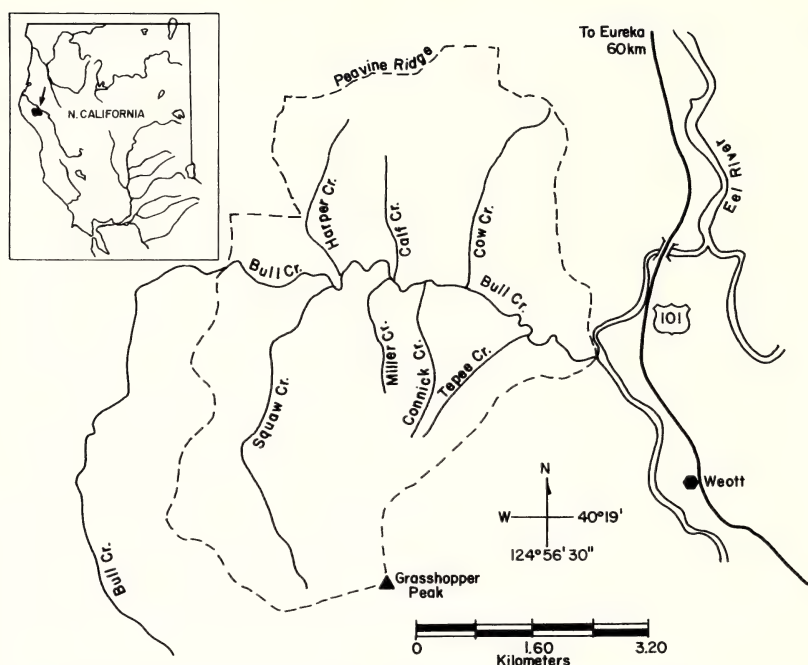


FIG. 1. Location of the study area in the Bull Creek watershed, Humboldt Redwoods State Park, northwestern California.

between 1955–1974, Gripp (1976) found that 89% were associated with three major synoptic weather systems: the Pacific High (post-frontal), the Great Basin High, and the Subtropical High Aloft pattern. These weather patterns can be expected to occur 50–55 days per summer fire season (Hull et al. in Gripp 1976). The greatest number of days of critical fire weather can be expected to occur in July, August, and September. Sixty-nine percent of the large fires (1955–1974) in Humboldt and Del Norte cos. occurred during August and September (Gripp 1976).

STUDY SITE

This study was conducted in a ca. 3500 ha old-growth *S. sempervirens* and *Pseudotsuga menziesii* forest growing in the Bull Creek watershed of Humboldt Redwoods State Park, California (Fig. 1). The forest includes the Rockefeller Forest that occurs 35 km east of the coast and experiences none of the moderating influence of the Pacific Ocean on summer temperature and humidity to the same extent as do the coastal *S. sempervirens* groves to the north. Inland sites typically have summer temperatures between 20–30°C and relative humidities between 40–50%, whereas coastal sites experience

summer temperatures of 15–18°C and relative humidities between 80–90% (Horn 1966, Azevedo and Morgan 1974, Elford and McDonough 1974). Summer fog flowing up the Eel River Valley often drifts into the Bull Creek watershed. Fog, however, occurs less frequently in the Rockefeller Forest than it does in *S. sempervirens* groves along the Eel River or closer to the ocean (Waring and Major 1964, Azevedo and Morgan 1974). As a result, the Bull Creek drainage experiences greater diurnal and annual temperature extremes. Summer droughts are common with nearly all of the 760–2500 mm of precipitation falling as rain from October to April.

The watershed's topography is varied with slopes from 0% to more than 50%. Elevations range from 50 m at the mouth of Bull Creek to roughly 1030 m. Potential fire hazard is higher in the Bull Creek watershed than in coastal *S. sempervirens* because of the steep slopes and relatively severe summer fire weather.

Nearly pure stands of *S. sempervirens* are found along the alluvial flats of Bull Creek. Occasional overstory associates include *Abies grandis* and *P. menziesii*. Understory associates include *Lithocarpus densiflorus*, *Umbellularia californica*, *Vaccinium ovatum*, *Gaultheria shallon*, *Polystichum munitum*, and *Oxalis oregana*.

On the slopes above the alluvial flats, the density and basal area of *S. sempervirens* declines with increasing elevation, although this species dominates (greatest basal area) nearly everywhere it is found. At lower elevations, *S. sempervirens* is associated with *P. menziesii*, *A. grandis*, *L. densiflorus*, *A. menziesii*, and *U. californica*. On rocky sites or near prairies, *Quercus garryana* and *Q. kelloggii* are found. At higher elevations, *A. grandis*, *U. californica*, *Q. garryana*, and *Q. kelloggii* are absent or rare, whereas *L. densiflorus* and *A. menziesii* increase in density and basal area. *Lithocarpus densiflorus* saplings and *V. ovatum* thickets are found in the understory at all slope elevations.

LAND USE HISTORY

Pre-settlement period (pre-1875). Pre-settlement fires in the Bull Creek watershed probably were caused mostly by Indians. Lightning activity in this part of the range of *S. sempervirens* is relatively low, but it is often accompanied by rainfall when it does occur (Fritz 1931). The Sinkyone Indians were the primary inhabitants of this region. They migrated through the watershed on their way from the South Fork of the Eel River to the Pacific Ocean and had established villages in and near the watershed. Regular burning by the Sinkyones has been reported as a means to drive out insects and rodents for food and to keep the forest understory open for travel (Fritz 1931, Gilligan 1966).

Settlement period (1875–1897). European man arrived in the vicinity of Bull Creek in 1848 when four members of Dr. Josiah Gregg's expedition from Weaverville to San Francisco proceeded up the South Fork of the Eel River. It was not until the early 1870's, however, that settlement occurred. One of the earliest settlers was Tosaldo Johnson who grazed sheep and cattle on prairies in what is now known as the Rockefeller Forest. By 1895, most of the Bull Creek watershed had been claimed under provisions of the Homestead Act. Fire was used by early settlers for the maintenance and enlargement of pastures and for land clearing (Gilligan 1966). Many fires escaped into the forests because of the lack of organized fire suppression.

Post-settlement period (1898–1940). The major land use activities from 1895–1945 were livestock grazing, farming, debarking of *L. densiflorus* for tannin production, and logging of *P. menziesii* and *S. sempervirens*. Broadcast burning was used regularly during this period to maintain pastureland (Gilligan 1966), and to facilitate logging activities. Logged areas were burned commonly prior to log skidding to reduce the impediments of logging debris and understory vegetation (Fritz 1931). Many of these fires burned into old-growth *S. sempervirens* stands, but apparently were extinguished naturally because of a combination of lower temperatures, higher relative humidities, and high fuel moisture contents. In years when the fuels were especially dry and the weather hot or windy, however, fire readily spread through the *S. sempervirens* forest. For example, in 1936 a fire spread southward from a broadcast burn on property of the Pacific Lumber Company into an old-growth *S. sempervirens* forest in the Bull Creek watershed (unpubl. fire report, Calif. Dept. of Forestry 1936). In 1936, there were many other fires burning in old-growth *S. sempervirens* forests on the north coast of California. Although fire archives of the California Department of Forestry probably do not contain all of the fire reports for 1936, the existing reports indicate that there were fires that covered from 86–4856 ha in areas of old-growth *S. sempervirens* in Humboldt and Del Norte cos. All of these fires originated from escaped broadcast burns or other incendiary activities.

After 1945, land use patterns changed with the implementation of the State Forest Practices Act and with more vigorous fire suppression. As a result, the number of escaped fires from agricultural or logging activities has been reduced greatly.

METHODS

The test to verify that basal sprouts can be used to determine fire frequency was conducted in northern Humboldt Co., 130 km north

of the main study area. All other data were collected in the Bull Creek watershed, Humboldt Redwoods State Park.

Basal sprout ages and fire frequency. Establishment dates of basal sprouts were determined in three areas of old-growth *S. sempervirens* that are known to have experienced fires. One of the areas burned in October 1974 along a tributary of Redwood Creek in Redwood National Park (RNP), and the other two areas burned during a fire of late September 1936 near the northern boundary of Prairie Creek State Park. The exact location of the 1974 fire was determined from records on file at RNP and by eyewitness accounts (Veirs, pers. comm. 1983). Locations of the two areas in the 1936 fire were determined using a fire report (unpubl. fire report, Calif. Dept. of Forestry 1936), and re-establishing photo points used in the taking of photographs following the fire (photos on file at RNP). A total of 20 basal sprouts from different parent trees were dated from the three areas: 10 from the 1974 fire, and five from each of the two 1936 fire areas. Basal sprouts were sampled next to trees that had bark char or fire scarring, and those sprouts that had no external evidence of fire. Increment corings were extracted at a height of 15 cm, cross sections were removed approximately 10 cm above ground level, and both were sanded and examined under a microscope. A correction factor of one year was added to the dates determined by counting annual rings.

Fire history study. Fifty-nine sample points were established in a 0.80 km² grid pattern in the 3500 ha old-growth *S. sempervirens* and *P. menziesii* forest that occurs in the eastern portion of the Bull Creek watershed. All trees of *S. sempervirens* within a 150 m radius of the sample point were examined for basal sprouts and evidence of past fires. Any sprout whose parent had a fire scar or bark char was assumed to have resulted from a fire. There were often two and three generations of basal sprouts evident from one parent tree (Fig. 2). The number of sprouts age class⁻¹ parent tree⁻¹ was variable, but usually was only one or two. Increment cores were extracted from basal sprouts of all apparent age classes as close to the base of their stems as possible, although usually within 25 cm of ground level. The cores were mounted in permanent holders, sanded, and examined under a microscope.

Dates of sprout establishment were determined by summing the number of years counted on the extracted increment cores to the mean annual height growth of basal sprouts. Mean basal sprout height growth for the first year following three prescribed burns near Look Prairie was 37 ± 11.7 (s.e.) cm (Stuart 1986). Crossdating was attempted, but was found to be ineffective primarily because of strong competitive interactions and variable radial growth patterns.



FIG. 2. Two generations of *Sequoia sempervirens* basal sprouts. Parent tree has a fire scar at its base, and charred bark extending approximately 10 m up its stem.

Studies in *S. sempervirens* by Douglass (in Schulman 1940), Schulman (1940), and LaMarche and Wallace (1972) have found similar difficulties in crossdating *S. sempervirens* cross sections. Fire dates were recognized if there was synchrony among basal sprout dates. To help substantiate the basal sprout fire dates, increment corings were extracted from adjacent *P. menziesii* and *A. grandis*. It was assumed that these species became established following the liberation of growing space by a fire. A similar pattern was observed by Veirs (1982) in *S. sempervirens* stands that occur 150 km to the north of the study site, where *P. menziesii* and *Tsuga heterophylla* became established after ground fires.

Additional fire dates were obtained by dating fire scars on stumps found in an old clearcut. All but one of the several clearcuts that were scattered throughout the forest were cut too long ago and yielded rotten, unusable stumps. A 35-year-old clearcut unit on a north-west aspect, however, was found whose stumps were sound enough to be used. Following a reconnaissance, five stumps were found showing two or more fire scars. Crossdating was performed for those stumps with uninterpretable sapwood rings using fire intervals established with *S. sempervirens* basal sprouts.

The original objective of determining exact historic fire boundaries could not be achieved because equal-aged basal sprouts from individual trees were dispersed too widely. Some reasons for this were: 1) the density of *S. sempervirens* on slopes was relatively low (10–40/ha); 2) not every *S. sempervirens* sprouted following fire, leading to highly dispersed equal-aged basal sprouts; and 3) some basal sprouts were killed by subsequent fires, which led to even greater dispersion of equal-aged basal sprouts. In spite of these factors, two estimates of fire size were attempted based on aspect and position within the Bull Creek watershed. Eleven zones were delimited (Table 1) to represent areas of similar aspect and watershed position. The first estimate of fire size was a liberal one based on the assumption that an entire watershed zone burned if there was any evidence of fire in that zone. Fire size was then estimated by summing the areas of those fire affected zones. Although this technique overestimates fire size for small local fires, it is probably realistic for many pre-settlement and unsuppressed fires. Those fires likely burned for weeks at a time, especially during drought periods, and were extensive. Many of the large 1936 fires, for example, in *S. sempervirens* forests on the north coast of California, burned for 2–3 weeks even with fire suppression (unpubl. fire reports, Calif. Dept. of Forestry 1936). The second estimate of fire size was more conservative. I assumed that, for a watershed zone to burn completely, it must have had more than one plot with evidence of fire. For those watershed zones having only one plot with evidence of fire, I assumed that the fire

TABLE 1. ZONES REPRESENTING AREAS OF SIMILAR ASPECT AND WATERSHED POSITION WITHIN THE OLD-GROWTH PORTION OF THE BULL CREEK DRAINAGE. Mean pre-settlement fire intervals for each zone are presented (data are $\bar{x} \pm \text{s.e.}$).

Fire zones	Area (ha)	Aspect	Mean fire interval
Harper Creek	368	S	21.8 (6.7)
Calf Creek	337	S	31.0 (12.1)
Western Cow Creek	397	SE	23.4 (11.6)
Eastern Cow Creek	433	SW, W	34.8 (8.4)
Tepee Creek	286	NE	19.5 (4.9)
Connick Creek	190	N	43.7 (14.2)
Miller Creek	223	N	36.3 (25.3)
Lower Eastern Squaw Creek	261	NW	11.3 (6.7)
Upper Eastern Squaw Creek	410	NW, W	21.0 (5.1)
Lower Western Squaw Creek	257	NE, N	18.2 (3.3)
Upper Western Squaw Creek	348	NE, E	21.8 (9.2)
	3510		24.6 (2.8)

burned $\frac{1}{59}$ of the entire study area, i.e., 3500 ha/59 plots = 59.3 ha. Once fire size was estimated, I calculated conservative and liberal estimates of the fire cycle for the post-settlement (1898–1940), settlement (1875–1897), and pre-settlement periods (pre-1875). The fire cycle is defined as the length of time necessary for an area equal to the entire area of interest to burn (Romme 1980).

RESULTS

Basal sprout ages and fire frequency. Dates of basal sprout establishment in the three sampling areas verified the known fire dates. In the area of the late season 1974 fire, nine out of 10 basal sprouts were determined to have been established in 1975, with the other basal sprout dated at 1976. Similar results were found in the two sampling areas in the area of the late season 1936 fire. Eight out of 10 basal sprouts were dated to 1937; one was dated to 1938; and one was found to have been established in 1940.

Fire history study. Fire frequencies for the pre-settlement, settlement, and post-settlement periods were calculated for individual watershed zones, the entire study area, and for the 35-year-old clear-cut (fire scars only). The pre-settlement mean fire interval for the 11 watershed zones ranged from 11.3 ± 6.7 (s.e.) yr to 43.7 ± 14.2 (s.e.) yr (Table 1). There were no statistically significant differences ($p > 0.05$) between the pre-settlement mean fire intervals of the watershed zones. The average of the mean pre-settlement fire intervals of the 11 watershed zones was 24.6 ± 2.8 (s.e.) yr. Shorter mean fire intervals were found for the settlement [15.6 ± 1.5 (s.e.) yr] and the post-settlement [7.8 ± 0.6 (s.e.) yr] periods. No statistically significant differences ($p > 0.05$) were found between the mean fire

TABLE 2. FIRE DATES AND FIRE INTERVALS DETERMINED FROM *Sequoia sempervirens* BASAL SPROUTS, CONIFER (*Pseudotsuga menziesii* AND *Abies grandis*) ESTABLISHMENT DATES, AND FIRE SCARS IN THE OLD-GROWTH PORTION OF THE BULL CREEK DRAINAGE.

	Fire year	No. of fire scars	No. of basal sprouts	No. of conifers est.	Fire interval (yr)
Post-settlement period	1940	2	3	1	4
	1936	—	11	2	6
	1930	—	8	—	3
	1927	—	4	1	4
	1923	1	5	—	4
	1919	—	13	6	6
	1913	1	3	1	4
	1909	—	6	4	5
	1904	—	8	5	6
	1898	2	6	1	3
Settlement period	1895	—	4	2	7
	1888	—	15	4	5
	1883	—	6	3	8
	1875	—	4	5	10
Pre-settlement period	1865	1	6	4	8
	1857	—	7	5	11
	1846	—	5	6	11
	1835	4	5	4	9
	1826	—	3	3	9
	1817	—	4	1	15
	1802	1	7	5	18
	1784	—	5	—	20
	1764	2	—	—	16
	1748	—	5	1	9
	1741	2	2	—	15
	1726	—	6	—	19
Incomplete data	1707	2	—	—	12
	1695	—	2	—	9
	1686	—	2	—	38
	1648	—	2	—	37
	1611	—	2	—	13
	1598	1	1	—	12
	1586	—	1	—	17
	1569	1	—	—	63
	1506	—	1	—	11
	1495	—	1	—	26
	1469	—	1	—	139
	1330	1	—	—	—

intervals of the eleven watershed zones for either the settlement or post-settlement periods.

Considerable variability was found in fire intervals within watershed zones and between the fire intervals of all watershed zones.

Pre-settlement fire intervals varied from 8–87 yr. The coefficients of variation for pre-settlement fire intervals for individual watershed zones ranged from 36–120% and for the means of fire intervals of all watershed zones it was 37.8%.

Fire intervals calculated for the entire study area in each fire year and averaged for the three time periods are shown in Table 2. The post-settlement period had the lowest mean fire return interval [4.5 ± 0.6 (s.e.) yr], with the settlement period, and pre-settlement periods having longer intervals [7.5 ± 0.8 (s.e.) yr, and 13.3 ± 1.2 (s.e.) yr, respectively]. Statistically significant differences ($p < 0.05$) were found between the fire interval means for all three time periods.

The fire intervals calculated from the fire scar data exhibited a similar trend as the other two estimates, with a longer fire interval [31 ± 3.1 (s.e.) yr] in the pre-settlement period and a shorter fire interval [14 ± 2.0 (s.e.) yr] for the post-settlement period. There were no fire scars found for the settlement period.

No statistically significant differences ($p > 0.05$) between time periods and either the conservative or liberal estimates of fire size were found. Mean fire size based on the conservative estimate for the post-settlement period was 918 ± 162 (s.e.) ha, for the settlement period 1097 ± 362 (s.e.) ha, and for the pre-settlement period 786 ± 139 (s.e.) ha. The mean fire size based on the liberal estimate for the post-settlement period was 1748 ± 121 (s.e.) ha, for the settlement period 2018 ± 151 (s.e.) ha, and for the pre-settlement period 1629 ± 167 (s.e.) ha. Fire frequency was not correlated with either the conservative or the liberal estimates of fire size ($r = -0.215$, $p = 0.100$; $r = -0.254$, $p = 0.100$, respectively). Fire cycles calculated using the conservative estimate of fire size were 51.6, 16.0, 16.0 yr for the pre-settlement, settlement, and post-settlement periods. The fire cycles using the liberal fire size estimates were 26.2, 10.0, and 9.5 yr for the same periods. A comparison of the five estimates of fire frequency are presented in Table 3.

DISCUSSION

Fire frequency based on watershed zones, the entire study area, fire scars, and two estimates based on the fire cycle were all similar. Each of these methods revealed a pattern of relatively long fire intervals during the pre-settlement period, shorter fire intervals during the settlement period, and still shorter fire intervals during the post-settlement period. The mean pre-settlement fire intervals for all the watershed zones (24.6 yr), and for the area with fire scars (31 yr) were similar to those reported by Fritz (1931; ca. 25 yr) and Jacobs et al. (1985; 22–27 yr). The shorter pre-settlement fire interval based on the entire study area (13.3 yr) was an artifact of the size of the reference area. A large sampling area is likely to include more

TABLE 3. ESTIMATES OF FIRE FREQUENCY FOR THE OLD-GROWTH PORTION OF THE BULL CREEK WATERSHED. Frequency estimates are presented for the post-settlement, settlement, and pre-settlement periods. Fire interval data are $\bar{x} \pm \text{s.e.}$

	Post-settlement	Settlement	Pre-settlement
Fire interval (yr)			
Based on entire study area	4.5 (0.6)	7.5 (0.8)	13.3 (1.2)
Based on scars from 1 site	14.0 (2.0)	—	31.0 (3.1)
Based on watershed zones	7.8 (0.6)	15.6 (1.5)	24.6 (2.8)
Fire cycle (yr)			
Conservative estimate	16.0	16.0	51.6
Liberal estimate	9.5	10.0	26.2

evidence of past fires than a smaller one (Arno and Petersen 1983). My entire study area, for example, was 3500 ha, whereas the largest watershed zone was only 433 ha. The studies by Fritz, Veirs (1982), and Jacobs et al. were conducted in areas less than 100 ha.

Fire frequency estimates based on the fire cycle should be considered only as estimates because I was unable to reconstruct exact fire perimeters. The liberal estimate of the fire cycle (26.2 yr) should be considered the probable minimum time; and the conservative estimate (51.6 yr) should be considered as the probable maximum time. It is unlikely that the true fire cycle, especially for the pre-settlement period, is greater than my conservative estimate because pre-settlement fires were not suppressed and, therefore, were probably more extensive.

Pre-settlement fire frequencies were highly variable and no significant differences were found between pre-settlement mean fire intervals among the eleven watershed zones. These phenomena are probably due to large variances within and between watershed zones and the small number of intervals in each watershed zone. Ecological and land management inferences based solely on pre-settlement mean fire intervals would be simplistic. Any prescribed burning program designed to recreate pre-European man fire regimes should incorporate variable intervals between fires (McBride et al. 1986) within and between watershed zones.

The longer fire intervals (50–500 yr) reported by Veirs (1982) can be attributed to the relatively mild fire weather conditions found in coastal *S. sempervirens* forests (Elford and McDonough 1974, Gripp 1976). Differences in fire frequency throughout the range of *S. sempervirens* are apparently a function of the steep climatic gradient extending from the cool, moist coastal sites to the relatively warm, dry inland sites.

ACKNOWLEDGMENTS

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ANNOUNCEMENT

VASCULAR PLANTS OF ARIZONA

Taxonomists interested in the flora of Arizona have convened several times since summer 1986 to organize a working group to produce a new plant identification manual for the state. Because *Arizona Flora* by Kearney and Peebles is out-of-print, a seminar intended for potential users was hosted by the Herbarium of the University of Arizona at Tucson, addressing the subject, "Revising *Arizona Flora*: What do you want?" in discussion format.

As a result of the seminar an editorial board, consisting of Frank S. Crosswhite, editor-in-chief, Richard S. Felger, Charles T. Mason, Jr., Donald J. Pinkava, John R. Reeder, and Rebecca K. Van Devender, has been established. It will govern all stages of production from planning to actual printing and publication. Several decisions have been made. The new book will be entitled *Vascular Plants of Arizona* and will be consistent in size, shape and complexity with *Gray's Manual of Botany*, although not necessarily consistent in style and format. The editors wish the book to include the works of the most highly qualified experts for each taxonomic group and solicit communication with all interested in contributing. Treatments accepted and published will be acknowledged with an authorship by-line. Guidelines for authors are being prepared and will be available from Rebecca K. Van Devender, Herbarium, College of Agriculture, University of Arizona, Tucson 85721.

CHROMOSOME RACES OF *GRAYIA BRANDEGEI* (CHENOPODIACEAE)

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ABSTRACT

Diploid ($2n = 18$) and tetraploid ($2n = 36$) races of *Grayia brandegei* differ in phenotype and geographic distribution. Diploids have narrow, linear leaves and mostly are restricted to south-central Utah and northeastern Arizona. Tetraploids are larger statured, bear larger, more oval leaves and mostly occur in isolated populations in northeastern Utah, south-central Wyoming, eastern Colorado, and northwestern New Mexico. Because of their morphological and distributional differences, the tetraploid form is designated as a new variety, *Grayia brandegei* var *plummeri*.

Grayia brandegei was described by Asa Gray (1876) from specimens obtained by Brandegee on the banks of the San Juan River in Utah, near the border of Colorado. It differs from the only other species in the genus, *G. spinosa* Moq., in several morphological features and geographic distribution. Whereas *G. spinosa* has a widespread distribution throughout western United States, *G. brandegei* is limited mostly to the drainage of the Colorado River in eastern Utah and adjacent states. Their ranges overlap in several places and appear to be separated primarily by edaphic differences.

Grayia brandegei usually grows on heavy clay soils or sandy loams, but is not restricted to the Chipeta formation, as suggested by Colotzi (1966). Like most other shrubs of the Chenopodiaceae, except *Atriplex*, it lacks Kranz-type leaf anatomy and presumably has the C_3 photosynthetic pathway. Contrary to previous reports, it is monoecious rather than dioecious. Leaves appear in early April, before flowering, and abscise in late summer.

Some populations of *G. brandegei* contain large robust plants with broad, oval leaves, whereas others have smaller-statured plants with narrow, linear leaves. To determine the basis for interpopulational differences, comparative morphological and cytological studies were

TABLE 1. LOCATIONS OF POPULATIONS OF *Grayia brandegei* EXAMINED FOR CHROMOSOME NUMBER AND MORPHOLOGICAL FEATURES. Soil properties were examined for those populations marked with *.

Diploids	Tetraploids
*AZ, Apache Co., 16 km n. of Many Farms	*CO, Garfield Co., 12 km nw. of Rifle
*CO, Mesa Co., 16 km w. of Mack	NM, San Juan Co., 10 km n. of Aztec
*UT, Grand Co., 8 km nw. of Moab	NM, San Juan Co., 20 km se. of Bloomfield
*UT, San Juan Co., 16 km s. of Blanding	*NM, San Juan Co., 8 km e. of La Plata
UT, San Juan Co., 20 km se. of Hites Crossing	UT, Emery Co., 16 km e. of Fremont Jct.
UT, San Juan Co., 1 km w. of Ismay Trading Post	UT, Garfield Co., 1 km e. of Henrieville
*UT, San Juan Co., 6 km n. of Montezuma Creek	*UT, Kane Co., Cottonwood Wash, 1 km s. of Cannonville
	*UT, Sanpete Co., 10 km nw. of Sterling
	*UT, Uintah Co., 18 km e. of Roosevelt
	UT, Wayne Co., 3 km e. of Notom Exit 24
	UT, Wayne Co., 10 km n. of Baker Ranch, Thousand Lake Mt.
	*WY, Carbon Co., 3 km nw. of Baggs

made on plants that grow in each of 19 populations distributed throughout the range of *G. brandegei*.

METHODS

Chromosome counts were made from microsporocytes in male buds taken from plants in natural populations or from mitotic cells in root tips taken from actively growing seedlings that were germinated on blotter paper in Petri dishes. In each case, the tissues were fixed in aceto-alcohol (1:3, v/v) and stained in aceto-carmin for microscopic examination. Numbers were determined for at least two plants in each of the 19 populations listed in Table 1.

Measurements of plant height and width, and leaf length and width were made on 20 plants in each population. Because the plants are mostly iso-diametric, plant volume was determined by plant height $\times \pi(\text{plant diameter}/2)^2$. Plants measured were taken at random at intervals of six feet along a linear transect through each population. Each leaf measured was the largest leaf on a randomly selected twig taken from each plant. Morphological characteristics were compared between ploidy levels using one-way ANOVA (Table 2). Voucher specimens from each population are deposited at Brigham Young University (BRY).

Soil samples were obtained from the site within each population by mixing together five shovelfuls of soil taken at six-foot intervals in a randomly selected linear transect. Cations of the soils were

TABLE 2. MEAN AND STANDARD DEVIATIONS OF PLANT STATURE AND LEAF DIMENSIONS OF DIPLOID ($n = 140$) AND TETRAPLOID ($n = 240$) FORMS OF *Grayia brandegei*. Measurements are from 20 plants in each of the populations listed in Table 1. All values significant at $p < 0.0001$ except when indicated.

	$2n$	$4n$	F (df = 378)
Plant ht. (cm)	31.23 ± 10.14	37.03 ± 13.35	19.78
Plant w. (cm)	71.21 ± 28.28	84.46 ± 33.59	15.41
Plant vol. (dm^3)	127.22 ± 97.21	307.66 ± 263.04	13.69
Leaf l. (mm) ^{ns}	34.86 ± 10.17	33.87 ± 13.04	0.60
Leaf w. (mm)	3.83 ± 1.47	9.13 ± 5.21	138.62
Leaf l/w ratio	9.59 ± 2.27	4.18 ± 1.67	708.21

analyzed in a Perkin Elmer 5000 Atomic Absorption Spectrophotometer. A saturated water extract was used for the analysis of the macronutrients Ca, Mg, K, and Na. The micronutrients Cu, Fe, Mn, and Zn were extracted in DTPA. P content was determined colorimetrically from a Na_2CO_3 extract. Na absorption ratio (SAR) was calculated from the values obtained for Na, Ca, and Mg. Cation exchange capacity (CEC) was determined by the ammonia distillation method. Texture was determined by the hydrometer method.

RESULTS

Cytological studies showed that plants in the population first collected by Brandegee in southeastern Utah near Ismay Trading Post were diploid with $2n = 18$ chromosomes. Diploid chromosome counts also were obtained from plants in six other populations (Table 1). In each population, the plants had narrow, linear leaves (Fig. 1, Table 2). In 12 other populations of *G. brandegei*, plants were more robust and had considerably wider leaves (Figs. 1, 2, 3, and Table 2). Those individuals examined were found to be tetraploid with $2n = 36$.

Tetraploid populations are more widely distributed than diploid populations (Fig. 3). Putative diploid populations, in which the plants are small-statured and bear narrow, linear leaves, are found along the San Juan River in southeastern Utah. Putative tetraploid populations, in which the plants are larger statured and bear wider leaves, are common in central and northeastern Utah, northwestern New Mexico and northwestern Colorado.

The only known population of *G. brandegei* outside the Colorado River drainage is located west of Sterling, Sanpete County, Utah. This sizeable tetraploid population is growing on Tertiary, Green River clays that are locally abundant, but are otherwise rare in the Great Basin drainage of Utah. This geological formation is common

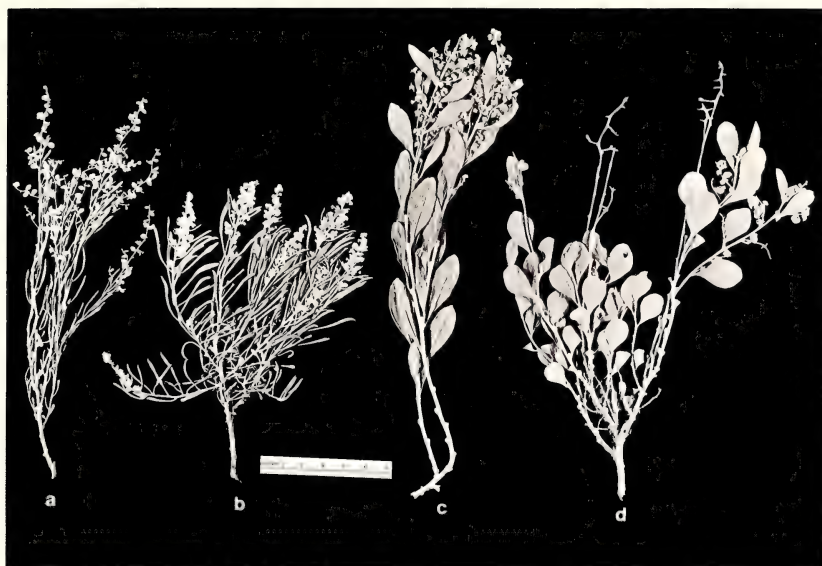


FIG. 1. Twigs of diploid (a, b) and tetraploid (c, d) *Grayia brandegei*. a. AZ, Apache Co., 16 km n. of Many Farms. b. UT, San Juan Co., 6 km n. of Montezuma Creek. c. WY, Carbon Co., 3 km nw. of Baggs. d. UT, Uintah Co., 18 km e. of Roosevelt.

in the northern portion of the Colorado Plateau, and some of the tetraploid populations in eastern Utah and western Colorado occur on it.

All macro- and micronutrients among populations noted in Table 1 showed no significant differences. Similarly pH, CEC, SAR, and soil texture showed no significant differences.

ANOVA for between-population differences for plant height and width and leaf length and width of 12 tetraploid populations were all significant (F-test, $p < 0.0001$).

DISCUSSION

The distribution pattern of diploid and tetraploid populations of *G. brandegei* in Utah, Wyoming, Colorado, Arizona and New Mexico suggests that the tetraploids were derived from the diploids. Because there are no other species that appear to have been involved in their origin, tetraploids are probably autotetraploids. Because of the conspicuous inter-population differences among them, they probably arose polyphyletically.

Repeated establishment of autotetraploid populations from diploid progenitors could be best explained as originating via triploids. Occasional triploids, arising in a diploid population from fertiliza-

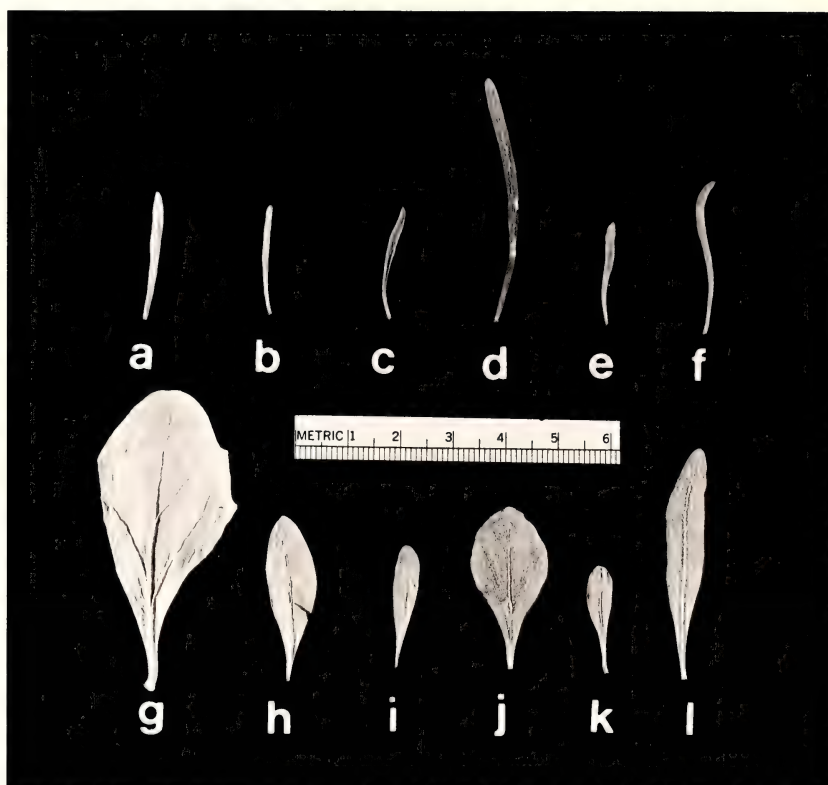


FIG. 2. Leaves of diploid (a-f) and tetraploid (g-l) *Grayia brandegei*. a. UT, Grand Co., 8 km nw. of Moab. b. UT, San Juan Co., 6 km n. of Montezuma Creek. c. UT, San Juan Co., 16 km s. of Blanding. d. CO, Mesa Co., 16 km w. of Mack. e. AZ, Apache Co., 16 km n. of Many Farms. f. UT, San Juan Co., 1 km w. of Ismay Trading Post. g. UT, Uintah Co., 18 km e. of Roosevelt. h. WY, Carbon Co., 3 km nw. of Baggs. i. UT, Sanpete Co., 10 km nw. of Sterling. j. UT, Emery Co., 16 km e. of Fremont Jct. k. CO, Garfield Co., 12 km nw. of Rifle. l. UT, Kane Co., 30 km s. of Cannonville.

tion of unreduced gametes, could generate bursts of additional triploids and tetraploids, because most aneuploid gametes from triploids are expected to fail. Progeny from triploids, therefore, would be diploids, triploids and tetraploids. The diploids would breed normally; the tetraploids would leave only triploid progeny; the triploids would again leave diploids, triploids and tetraploids. Consequently, there could arise, from an occasional triploid, self-accelerating bursts of triploids and tetraploids until sufficient tetraploids occurred to permit autonomous perpetuation.

Tetraploid plants of *G. brandegei* differ from diploids phenotyp-

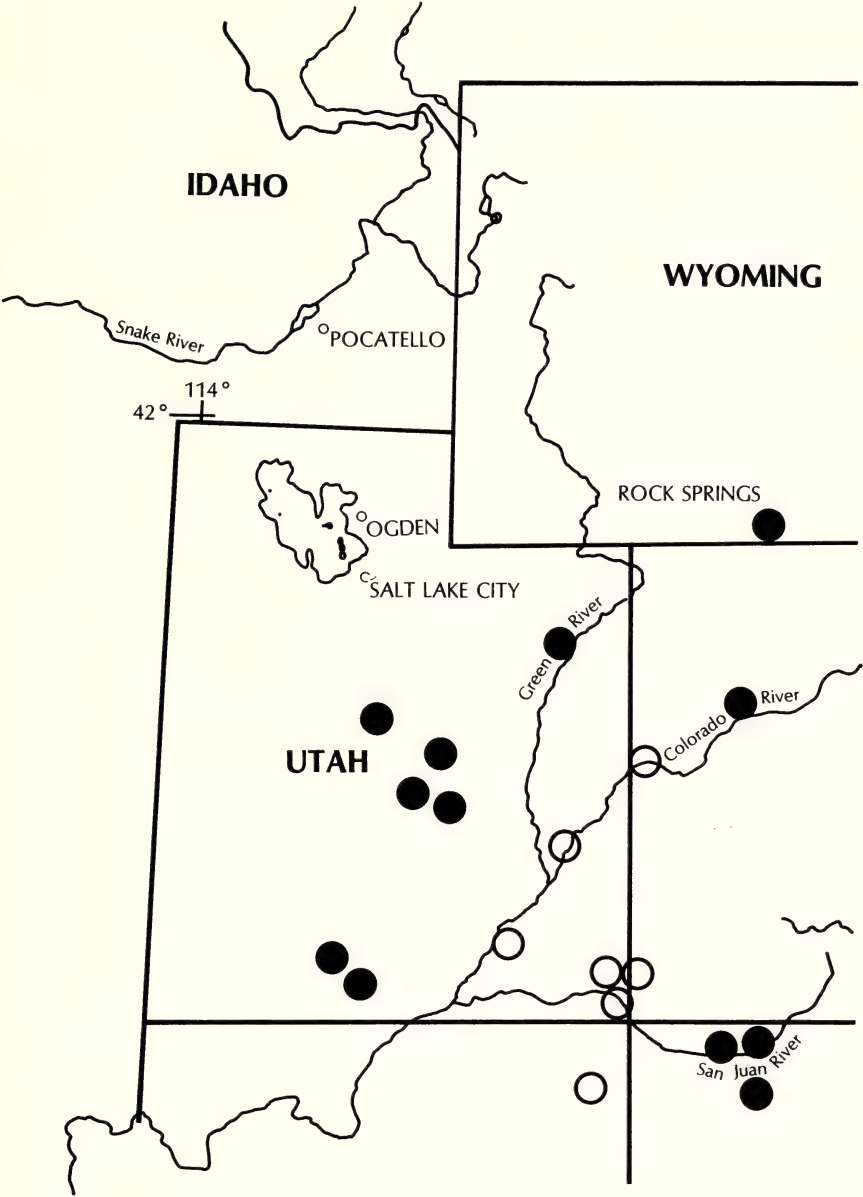


FIG. 3. Distribution of verified diploid and tetraploid forms of *Grayia brandegei*. Symbols: ○ = 2X, ● = 4X.

ically, particularly in stature and leaf-width, and have different geographic distributions, and so we propose them as a distinct variety.

Grayia brandegei A. Gray var. **plummeri** Stutz and Sanderson, var. nov.

Similis var. *brandegei* sed foliis latoribus, plantis altioribus, latoribus et tetraploideis differt, chromosomatum numerus $2n = 36$.

Erect shrub 6–14 dm high, 2.4–6 dm broad; branches erect or ascending, densely and finely pubescent. Leaf blades elliptic, ovate, obovate or oblanceolate, 2.5–6 cm long, 5–22 mm wide, apex obtuse or rounded. Leaf-anatomy non-Kranz. Heterodichogamously monotecious. Male inflorescence glomerulate, the glomerules borne in axils of leaves or small bracts; perianth 4–(5) parted, segments membranaceous, obovate; stamens 4(5), filaments subulate, anthers didymous, included. Female inflorescence paniculate, the flowers borne in axils of leaves or small bracts; bibracteolate, bractlets 5–6 mm wide, orbicular, completely united, margins extended into two wings 4–8 mm broad; perianth lacking; stigmas 2, filiform; utricle orbicular, compressed, included in the two bracts; pericarp membranaceous, free. Seed orbicular, 2–4 mm broad, erect; testa thin, membranaceous; embryo annular; endosperm copious; radicle inferior. Chromosome number: $2n = 36$.

TYPE: USA, UTAH, Duchesne Co.: ca. 18 km e. of Roosevelt, 31 Aug 1984, *Stutz 9325* (Holotype: BRY).

PARATYPES (all deposited in BRY): USA, CO, Garfield Co.: ca. 12 km nw. of Rifle, 18 Aug 1979, *Stutz 8478*. Moffat Co.: Sand Wash near Dugout Draw, T10N R97W S28, 31 Aug 1982, *Parks 908*. Rio Blanco Co.: 25 km e. of Rangely on US 64, 7 Jun 1965, *Collotzi 551*. NM, San Juan Co.: Angel's Peak badlands, ca. 20 km se. of Bloomfield, 5 Jun 1985, *Stutz 9438*. UT, Daggett Co.: East Grindstone Spr., e. end of Antelope Flat, T3N R22E S24, 6600 ft, 29 Aug 1978, *Neese and England 6648*. Emery Co.: I-70, ca. 16 km e. of Fremont Jct., 10 Sep 1983, *Stutz 9153*. Garfield Co.: 1 km e. of Henrieville, 20 Jun 1986, *Stutz 94337*. Kane Co.: Cottonwood Wash, ca. 12 km n. of US hwy 89, 12 Sep 1971, *Atwood and Kaneko 3319*. Sanpete Co.: clay hills w. side antelope valley, 10 km nw. of Sterling, 21 May 1984, *Stutz 9245*. Uintah Co.: ca. 18 km e. of Roosevelt, 25 May 1985, *Stutz 9430*. Wayne Co.: 3 km e. of Notom Exit, Hwy 24, 20 Jun 1984, *Stutz 9374*. WY, Carbon Co.: 3 km nw. of Baggs, 1 Sep 1984, *Stutz 9330*.

The varietal name is chosen to honor A. Perry Plummer who has pioneered numerous important studies of shrubs in western North America. He also discovered the only known population of *Grayia brandegei* growing in the Great Basin (Utah, Sanpete Co., 10 km w. of Sterling, 21 May 1984, *Stutz 9245*).

ACKNOWLEDGMENTS

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ANNOUNCEMENT

GRADUATE STUDENT AWARDS

The Eleventh Graduate Student Meetings of the California Botanical Society were held Saturday 25 April 1987 at the University of California, Davis. Sixteen papers were presented and awards were presented to the following individuals:

Completed Research

First Place—Jon Hart, UC Davis

Second Place—George Robinson, UC Davis

Research in Progress

First Place—Bruce Baldwin, UC Davis

Second Place—Herb Saylor, San Francisco State University

Third Place—Sam Hammer

Proposed Research

First Place—Stacy Giles, San Francisco State University

Second Place—Barbara Gartner, Stanford University

Third Place—Mike Wood, San Francisco State University

Naill McCarten

Graduate Student Representative

ALLIUM SHEVOCKII (ALLIACEAE), A NEW SPECIES
FROM THE CREST OF THE SOUTHERN
SIERRA NEVADA, CALIFORNIA

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ABSTRACT

Allium shevockii, a new species from the crest of the southern Sierra Nevada on the Kern Plateau in Kern County, California is described and illustrated. The new species shows morphological similarities to *A. atrorubens*, *A. fimbriatum*, and *A. monticola* in the *A. sanbornii* alliance. It differs from these species in its obovate to oblanceolate perianth segments that are distinctly reflexed distally, and its long thread-like rhizomes that terminate in bulblets in addition to those produced at the base of the parent bulb.

A new species of *Allium* was discovered by James R. Shevock during floristic work in botanically unexplored and remote areas of the southern Sierra Nevada. Populations of this species are scattered over a relatively limited geographical area on Spanish Needle Peak along the crest of the southern Sierra Nevada. Due to the rugged nature of the habitat and limited access to this area, the full range of this new taxon can only be surmised. Review of *Allium* in major U.S. herbaria (CAS, DAV, DS, GH, JEPS, MO, NY, POM, RSA, UC, US, WS) failed to locate additional collections of it.

Allium shevockii McNeal, sp. nov.

Tunica exterior bulbi brunnea, reticulatione cellulari carens, tunice interiores luteolae, in sicco rubescentes; bulbi facientes rhizomata filiformia 3–10 cm longa facientia bulbos terminales vel facientes 1–2 bulbillos basales parientes rhizomata filiformia. Scapus (7–)10–20(–29) cm longus. Folium singulum, teres, 15–33 cm longa. Umbella 12–30 vel pluribus floribus. Segmenta perianthii alba ad pallide viridia infra, marronina in triente superiore; segmenta exteriora 12–14 mm longa et 4.5–6 mm lata, erecta, obovata ad oblanceolata, acuta ad mucronata, marginibus irregulariter et non profunde dentatis, reflexa et crispa ad apicem; segmenta interiora 11–13 mm longa et 4–4.5 mm lata, ovata, acuta, marginibus integris, latescentia ad apicem; stylus trilobus; ovarium manifeste cristatum 6 anguste triangularibus processibus, margines exteriores processuum undulatae ad non profunde et irregulariter dentatas (Fig. 1).

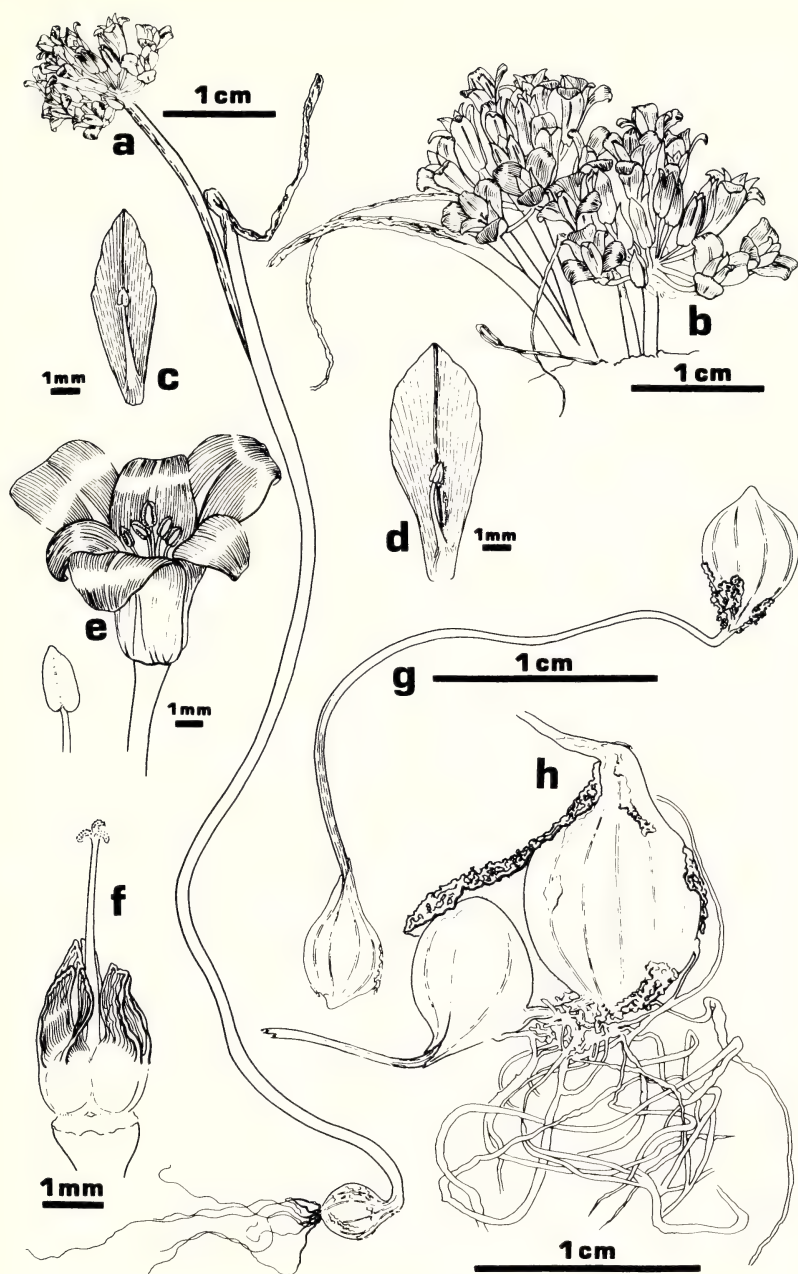


FIG. 1. *Allium shevockii* McNeal. a. Entire plant. b. Habit. c. Inner perianth segment. d. Outer perianth segment. e. Flower with anther. f. Ovary with prominent crests. g. Bulblet with rhizome and new bulb at tip (the lower bulb is the new one). h. Bulb with stipitate bulblet that has developed a rhizome. Drawn from *Shevock 11219* and 35 mm transparencies.

Bulbs subglobose, 10–15 mm long, outer bulb coat brown, lacking cellular reticulation, inner coats light yellow, turning reddish on drying, with obscure \pm quadrate cellular markings; bulbs forming thread-like rhizomes 3–10 cm long that develop terminal bulblets or forming 1 or 2 basal bulblets that produce thread-like rhizomes. Scape terete, succulent, fragile when fresh, (7–)10–20(–29) cm long; leaf one, terete, 15–33 mm long. Umbels 12–30 or more flowered; bracts usually 3 (rarely 2), 16–20 mm long, 5–8 mm wide, lanceolate, apiculate; pedicels 10–16 mm long. Outer perianth segments 12–14 mm long and 4.5–6 mm wide, erect, oblanceolate, acute to mucronate with irregularly shallow toothed margins, white to light green below, maroon on the reflexed, curled distal one-half; inner segments 11–13 mm long and 4–4.5 mm wide, ovate, acute, margins entire, white to light pink or maroon on the upper one-third, outwardly flared at the tip; stamens $\frac{1}{3}$ – $\frac{1}{2}$ as long as the perianth, anthers ca. 1 mm long, yellow, elliptic, mucronate; styles ca. equalling the stamens, three-lobed, ovary prominently crested with 6 narrowly triangular, radially oriented processes, processes emarginate, outer margins undulate to shallowly and irregularly toothed. Seed coat black with hexagonal, minutely pustuliferous cells. Chromosome number $n = 7$ (from the type collection).

TYPE: USA, CA, Kern Co.: W. slope of Spanish Needle Peak near summit, ca. 1.2 air km s. of the Tulare-Kern-Inyo Co. line, T25S R37E S4, 2315 m, 15 Jun 1985, *Shevock 11219* (Holotype: CAS; isotypes: CPH, NY, RSA).

PARATYPES: USA, CA, Kern Co.: From the type locality, 10 Jun 1986, *McNeal and Boyd 3155* (CAS, CPH, NY, RSA, UC); e. slope of Spanish Needle Peak, 2300 m, 10 Jun 1986, *Shevock, Norris, and Bagley 11636* (CAS, CPH, RSA, MO, NY, US).

Distribution, habitat, and phenology. *Allium shevockii* occurs in soil pockets on dark colored metamorphic (chlorite-chloritoid schist) outcrops, an adjacent igneous (aplite) intrusion, and on steep colluvial talus slopes between 2200–2350 m on Spanish Needle Peak in the southern Sierra Nevada, Kern Co., California. Bulbs mainly occur along the margins of outcrops where the slope is more stable. Reproduction appears to be primarily vegetative. Few mature flowers with developing capsules have been observed.

Vegetation in the general area is an open, mixed evergreen forest. Associates in the immediate vicinity are sparse due to the steep, unstable slopes. Associated species include: *Arabis davidsonii* Greene, *Arabis* sp., *Caulanthus pilosus* S. Wats., *Cercocarpus intricatus* S. Wats., *Dudleya calicicola* Bartel & Shevock, *Epilobium canum* (Greene) Raven subsp. *latifolium* (Hook.) Raven, *Eriogonum brendlovi* (J. T. Howell) Reveal var. *shevockii* J. T. Howell, *Eriogonum nudum* Dougl. ex Benth., s.l., *Eriogonum umbellatum* Torr., s.l.,

Eriogonum wrightii Torr. ex Benth. subsp. *subscaposum* S. Wats., *Eriophyllum ambiguum* (Gray) Gray var. *paleaceum* (Bdg.) Ferris, *Eriophyllum confertiflorum* (DC.) Gray, s.l., *Juniperus occidentalis* Hook., *Keckiella breviflora* (Lindl.) Straw, *Leptodactylon pungens* (Torr.) Rydb. subsp. *pulchriflorum* (Brand) Mason, *Mimulus* sp., *Pellaea mucronata* (D. C. Eat.) D. C. Eat., *Pinus monophylla* Torr. & Frem., *Quercus chrysolepis* Liebm., *Scrophularia desertorum* (Munz) R. Shaw, and *Symphoricarpos parishii* Rydb.

Allium shevockii is yet another highly restricted endemic from the southern Sierra Nevada. Habitat with similar slope, aspect, geology, and elevation occurs along the crest south of Spanish Needle to Mt. Jenkins, a distance of 6.5 air km. Access to this area will be enhanced greatly with the completion of the Pacific Crest Trail section that is currently under construction between Spanish Needle and the Owens Peak-Mt. Jenkins saddle. Suitable habitat north of Spanish Needle toward Sawtooth Peak and south of Mt. Jenkins toward Walker Pass along the crest appears to be lacking due primarily to a change in geology. In addition to the type locality, *A. shevockii* was located in six small, adjacent canyons on the west face and two canyons on the east face of Spanish Needle. These populations are composed of several thousand individuals. Approximately 10% of the suitable habitat has been surveyed at this time. All populations are free of human disturbances and are likely to remain so due to the rugged nature of the habitat.

Relationships. *Allium shevockii* belongs to the *A. sanbornii* alliance (Saghir et al. 1966) that is characterized by taxa having a single terete leaf per scape and a prominent ovarian crest with six processes (two per lobe). *Allium shevockii* possesses several features unique in the alliance including: 1) obovate to oblanceolate perianth segments, the outer series of which are strongly reflexed to coiled in the distal half; 2) the light-lemon yellow fresh bulb coats; 3) the long filamentous secondary rhizomes that develop from the main bulb or more commonly from basal bulblets that form on short, stout primary rhizomes at the base of the main bulb. These characters make *A. shevockii* distinctive and easily recognized.

The position of *A. shevockii* within the *A. sanbornii* alliance is problematical. In its formation of basal bulblets and more or less entire crest processes, it is similar to *A. atrorubens* S. Wats. and *A. monticola* A. Davids., but otherwise appears not to be related closely to either taxon that lack the secondary, filamentous rhizomes and distinctively reflexed outer perianth segments. In stature and the three-lobed style, it resembles *A. fimbriatum* S. Wats., s.l., but it seems not to be closely related to this taxon, which lacks both basal bulblets and filamentous rhizomes and has dentate to laciniate crest

processes. *Allium shevockii* apparently has evolved a series of unique features independent of other members of the *A. sanbornii* alliance.

ACKNOWLEDGMENTS

I thank James R. Shevock for specimens, information, photographs and field assistance, Dr. Robert Smutny of the Department of Classics, University of the Pacific, for assistance in preparing the Latin diagnosis and Sandra McNett-McGowan for preparing the drawings. I appreciate helpful reviews of the manuscript by Drs. J. Henrickson and L. V. Mingrone. Financial support for this research from the Faculty Research Committee and F. R. Hunter Memorial Fund of the University of the Pacific is acknowledged gratefully.

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ANNOUNCEMENT

NEW PUBLICATION

WEBER, W. A., *Colorado Flora: Western Slope*, Colorado Associated Univ. Press, 1334 Grandview Ave., Box 480, Univ. Colorado, Boulder 80309, 1987, 550 pp., 107 pl., 64 color pl., \$20.50. [Illustrated manual of vascular plants of the entire hydrological western slope of Colorado. Same format as *Rocky Mountain Flora*, with type faces reduced to accommodate more text. Introduction contains essays on floristic zones, pronunciation (European recommended!), common names (discouraged!), the Colorado-Altai plant geography connection, generic concepts (non-traditional!), eponymy. Keys to families, genera and species with derivations, glossary. Statements of habitat and endemic status. Families and genera alphabetical. Non-numerical index uses three-letter family acronyms. Controversial? Yes, indeed! Dedicated to Greene, Rafinesque, Rydberg, Camp, Shinnars, and Löve.

CLAYTONIA PALUSTRIS (PORTULACACEAE),
A NEW SPECIES FROM CALIFORNIA

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ABSTRACT

A new species of *Claytonia* (Portulacaceae) is described from the Sierra Nevada of California. Morphology, chromosome number, and distribution indicate a close relationship with *C. sibirica*.

Montia heterophylla (Torr. & Gray) Jepson was transferred to *Claytonia* by Swanson (1966) in his assessment of systematic relationships in the Montioideae (Portulacaceae). Jepson (1914) had indicated that the combination was based on *C. unalaschkensis* β *heterophylla* Nuttall. This was a manuscript name published by Torrey and Gray (1838) as a synonym of *C. alsinoides* γ *heterophylla* Torr. & Gray. Examination of the type of *heterophylla* (Nuttall s.n., "Oregon", NY!), shows it belongs to *C. sibirica* L., and differs from California collections upon which Jepson, Swanson, and others have based their usage of this epithet. The two collections cited by Jepson (Jepson 4884, JEPS; Hall and Chandler 304, UC) are stoloniferous, whereas the Nuttall specimen is not. Our further studies of the California plants, which in the past have been referred to *C. (Montia) heterophylla*, show that they represent a distinct species. This new species is differentiated easily from *C. sibirica* and from members of *Claytonia* sect. *Rhizomatosae* (*C. cordifolia* S. Watson, *C. nevadensis* S. Watson, *C. sarmentosa* C. A. Meyer, and *C. scammaniana* E. Hulten).

***Claytonia palustris* Swanson and Kelley, sp. nov.**

Herbae perennes, glabrae. Caules simplices, ca. 10–20 cm alti. Radix verticalis, stolones ex axillis foliorum producents. Folia caulesque virides; radix stolonesque albid. Inflorescentia terminalis, racemosa, floribus in axillis bractearum, numerosis. Ovarium postremo uniloculare, ovulis 3 (Fig. 1).

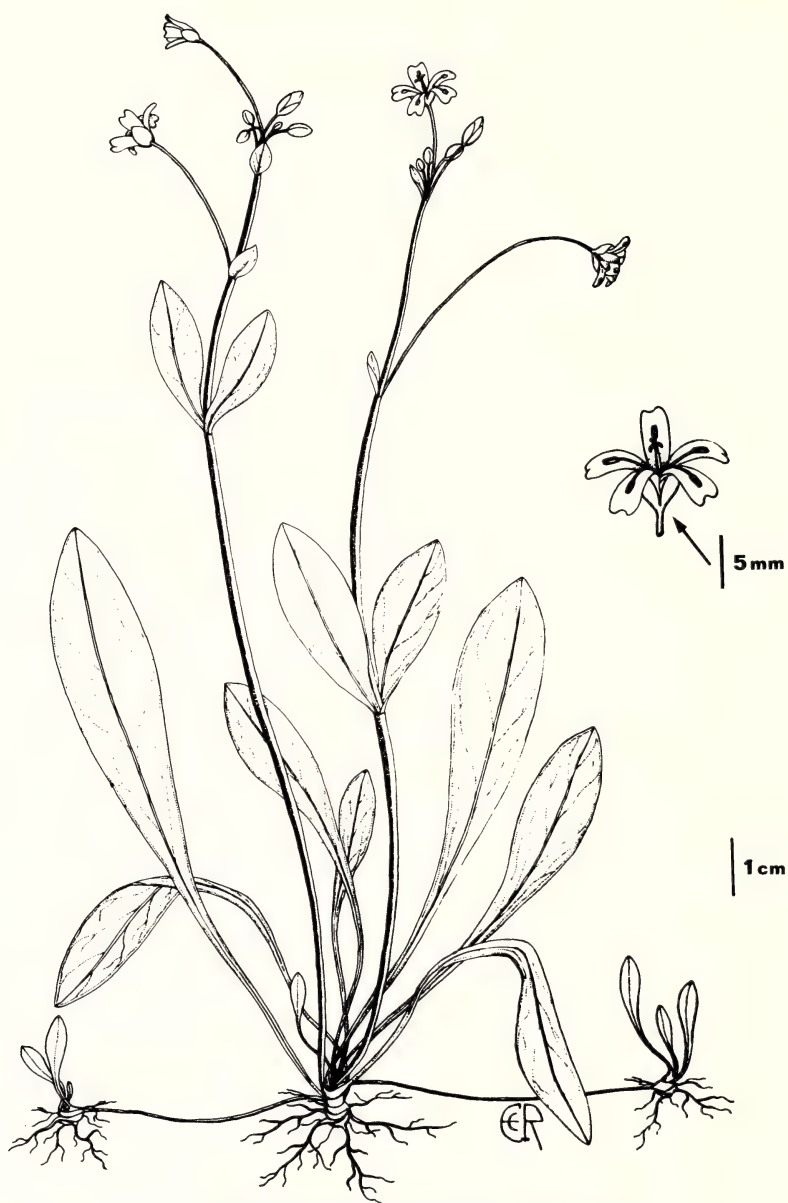


FIG. 1. *Claytonia palustris*. Drawn from Swanson 490.

Perennial glabrous herbs with white fleshy rootstalks 2–3 mm wide, 4–15 mm long. Stolons white, terete, 1–2 mm in diameter, 5–15 cm long, arising from the axils of the basal leaves. Basal leaves 1–10, lamina oblanceolate 3–4 cm long, 1–1.5 cm wide, petioles 5–10 cm long. Flowering branches several, 10–20 cm long; inflorescence terminal, racemose, 5–10 cm long, subtended by a pair of opposite, subsessile, slightly unequal, oblanceolate to narrowly elliptic leaves 0.5–1.5 cm wide, 2–5 cm long, sessile or tapering into a winged petiole. Flowers 5–12, each subtended by a sessile, ovate to elliptic bract, 1–3 mm wide, 3–8 mm long; sepals 2, 1–3 mm wide, 3–4 mm long; petals 5, oblong, white, emarginate, 5–9 mm long; stamens 5, opposite the petals, filaments 4–7 mm long, pollen 3-colpate; ovary unilocular at maturity, 2-valved, ovoid, 2–3 mm long; 1.5–2.5 mm wide; ovules 3; styles 3–5 mm long, style branches 3, each branch only partially stigmatic. Seeds 3, glossy, black. Chromosome number $n = 6$.

TYPE: USA, CA, Butte Co.: Jonesville, marshy, sloping, spring-fed meadow above s. bank of Jones Creek, 0.4 km e. of the Jonesville Hotel, 1550 m, 4 Jul 1959, *Swanson 490*, (Holotype: OSC; isotypes: CAS, CS, Mesa College, RSA, NY, SFV, UC).

PARATYPES: CA, Plumas Co.: Lake Almanor, 18 Jun 1920, *Clements s.n.* (CAS); Butterfly Valley, 23 Jun 1967, *Howell 42704* (CAS, OSU). Butte Co.: Chico Meadows, Sierra Nevada, 25 Jun 1915, *Heller 12022* (CAS); Jonesville, s. bank of Jones Creek, 0.4 km e. of Jonesville Hotel, 13 Jun 1959, *Swanson 477* (SFV). Fresno Co.: Pine Ridge, 15–25 Jun 1900, *Hall and Chandler 304* (UC); Frying Pan Meadow, s. fork of Kings' River, 12 Jul 1940, *Munz 15960* (RSA, UC). Tulare Co.: Sequoia National Park, vicinity of Alta Peak, 4 Aug 1896, *Dudley 1568* (DS); Jordan Hot Sprs., 18 Jul 1906, *Hall and Hall 8392* (UC); Cliff Creek, near junction of Timber Gap and Black Rock Pass trails, 31 Jul 1943, *Ferris and Lorraine 10944* (UC); Tule River, Sierra Nevada, *Pierson 1860* (RSA); Crescent Meadow, Sequoia National Park, 17 Jun 1956, *Tillett 464* (RSA); s. fork of middle fork of Tule River, 6 Jun 1974, *Gordon et al. 255* (SFV).

Claytonia palustris is characterized by a fleshy perennial stem 2–3 mm in diameter from which basal rosette leaves, stolons, scapose inflorescence branches, and adventitious roots arise. A distinctive feature of the species is the unequal length of the two opposite leaves that subtend the inflorescence, a phenomenon not found in any other *Claytonia* species.

Distribution and ecology. *Claytonia palustris* is endemic to California. It is known from two disjunct regions at opposite ends of the Sierra Nevada (Fig. 2) and from a third disjunct region in Siskiyou Co. (see Miller et al. 1984, Fig. 4). The species is largely restricted

to sunny areas, in wet meadows, marshy slopes, and streamside vegetation at mid elevations (1025–1650 m) in the north, and to mid and high elevations (1550–2450 m) in the south. Throughout most of its range, *C. palustris* does not overlap with the known distribution of *C. sibirica* s.l., the taxon with which it was confused by Jepson (1914) when he described the distribution of *M. heterophylla* as “Southern Sierra Nevada, 5700–7000 feet. Oregon to Alaska.” The Nuttall type locality, “Columbia Woods”, is within the range of *C. sibirica*, which is widespread in the northwestern United States, coastal British Columbia, Alaska, and the Aleutian and Commander Islands. Members of the *C. sibirica* complex extend southward into the California coast ranges to Santa Cruz Co., and eastward to Siskiyou Co. in the northern part of the state, where the complex overlaps the range of *C. palustris*.

The habitats in which *C. sibirica* s.l. is found in California and Oregon are moist but not marshy. *Claytonia sibirica* is adapted to growing in shaded habitats, whereas *C. palustris* is not. Many of the habitats occupied by *C. sibirica* are disturbed by natural causes or by man and it often grows as a ruderal plant. In Great Britain where *C. sibirica* was introduced in the last century, it has become widespread and is considered a weed (Salisbury 1961). Ruderal tendencies are not apparent in any of the populations of *C. palustris*.

The distribution of *C. nevadensis* approximates that of *C. palustris* (Fig. 2), although the individual populations are isolated geographically and ecologically. At similar latitudes, *Claytonia nevadensis* is found at higher elevations than *C. palustris*. The former is restricted to relatively pure stands, whereas *C. palustris* is found embedded in a dense tangle of perennial vegetation.

Claytonia cordifolia is widespread in the Pacific Northwest and extends southward into Siskiyou Co., California. Ecologically this species is similar to *C. sibirica* in its capacity to grow in shaded habitats, and to *C. palustris* in its ability to withstand competition from other vegetation. *Claytonia cordifolia* also is generally found in marshy or very moist situations.

Variation. Field and herbarium studies indicate that species of sect. *Rhizomatosae* are relatively uniform throughout their range. Chambers (1963) also noted the uniformity of *C. nevadensis* populations. *Claytonia sibirica*, however, is quite variable within and between populations. Miller et al. (1984) demonstrate that a euploid series exists in the taxon. The five species of sect. *Rhizomatosae* rely largely upon asexual reproduction by the use of branching rhizomes or stolons. Asexual reproduction is an adaptation common in plants living in climatically severe environments or where seedling establishment is difficult due to competition in closed communities (Stebbins 1950).

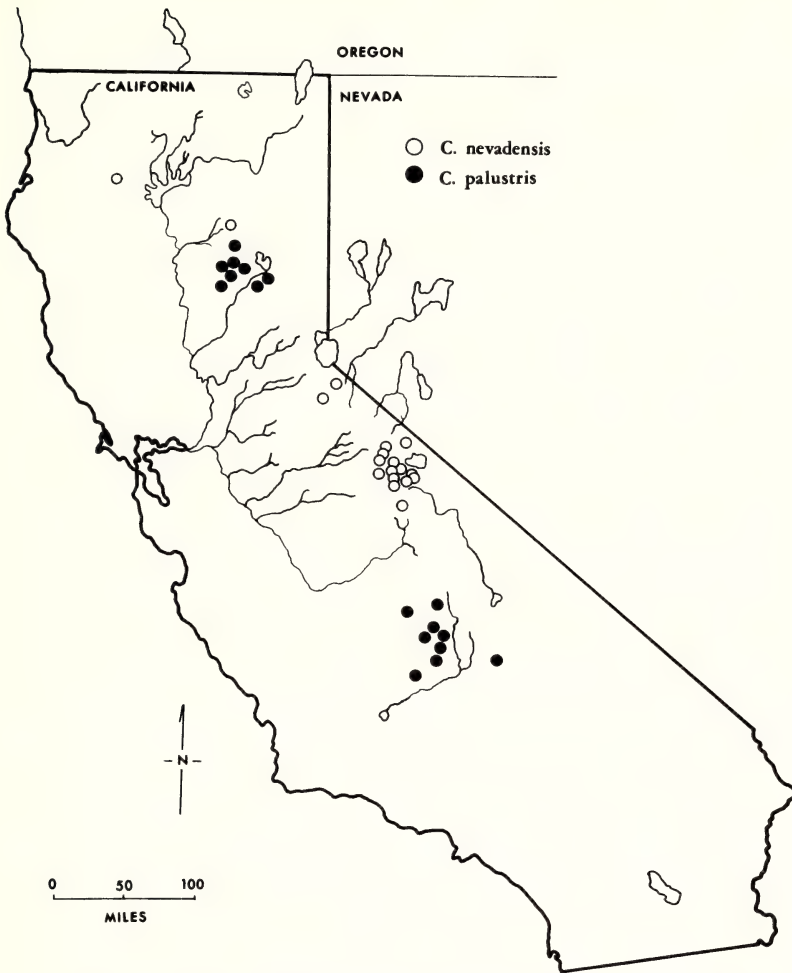


FIG. 2. Known localities for *Claytonia nevadensis* and *C. palustris*.

Chromosome counts. Previously unreported chromosome counts are given here; vouchers are deposited at SFV. Four collections of *C. palustris* (Butte Co., Swanson 477, 490; Plumas Co., Swanson 1047; Tulare Co., Swanson 1162) are all $n = 6$. Three populations of *C. nevadensis* are $n = 7$ (Lassen Co., Swanson 509; Mono Co., Swanson 1055, 1056). Counts were performed on three plants from each collection. All counts were made from anthers fixed in 3:1 ethanol-acetic acid and stored in 70% ethanol at 4°C until used. Meiosis was regular in all microsporocytes examined.

TABLE 1. CHARACTERS USED TO DIFFERENTIATE *C. palustris* AND CLOSELY RELATED SPECIES. See Lewis (1967) and Miller et al. (1984) for references to chromosome numbers not reported in this paper.

Species	Ovule number	Maximum seeds matured	Inflorescence bracts	Chromosome numbers	Runners or stolons
<i>C. cordifolia</i>	6	3	none	$n = 5$, $2n = 10_{II}$, 20_{II}	no
<i>C. nevadensis</i>	6	6	one	$n = 7$, $2n = 14_{II}$	yes
<i>C. palustris</i>	3	3	several	$n = 6$, $2n = 12_{II}$	yes
<i>C. sarmentosa</i>	6	6	none	$n = 7, 8$, $2n = 14_{II}$, 16_{II} , 28_{II} , 32_{II}	yes
<i>C. scammaniana</i>	6	6	none	unknown	unknown
<i>C. sibirica</i>	3	3	several	$n = 6$, $2n = 12_{II}$, 24_{II} , 36_{II}	infrequent

Relationships. In this paper, binomials are used to represent the nominal taxonomic species although different ploidy levels are known to exist within some of them and reproductive isolation is presumed to exist. The principal features we used to separate species of *Claytonia* are: 1) ovule number; 2) seed number; 3) ovule abortion; 4) number of bracts in the inflorescence (e.g., none, one subtending the lowermost flower, or several and each one subtending a flower); 5) base chromosome number; and 6) the presence or absence of stolons (Table 1).

Claytonia palustris shows similarities in these characters with members of sect. *Rhizomatosae* (*C. nevadensis*, *C. sarmentosa*, *C. scammaniana* and *C. cordifolia*) and members of *C. sibirica* s.l. (sect. *Caudicosae*). Jepson (1914, p. 474) referred to *C. palustris* accurately when he wrote (of *M. heterophylla*), "Stems . . . rising from tuberous rootstocks or cormlets, these sending out slender stolons that produce terminal cormlets, the secondary cormlets promptly producing leaves and flowers . . ." In these respects, *C. palustris* most closely resembles *C. nevadensis* and occasional plants of *C. sibirica*. Morphologically, there are greater differences between these species and *C. cordifolia* (Table 1). Our data suggest the close relationship of *C. palustris* and *C. sibirica*. In addition, similarities in flower size and morphology, leaf shape, leaf and stem texture, and plant and flower color support this suggested relationship. The occasional formation of stolons by *C. sibirica* (Swanson 1966) is quite similar to that in

C. palustris. The same base number ($n = 7$), six-ovuled flowers, pigmentation of vegetative parts and flowers, and texture of leaves suggest the affinity of *C. nevadensis* and *C. sarmentosa* and possibly *C. scammaniana* (chromosome number unknown). *Claytonia cordifolia* is isolated in sect. *Rhizomatosae* on the basis of chromosome number ($n = 5$). The regular abortion of three of the six ovules produced by each flower of *C. cordifolia* is an example of an evolutionary phenomenon that may have occurred independently in at least three groups in the genus (i.e., *C. sibirica*, *C. perfoliata* Donn ex Willd., and *C. spathulata* Dougl. ex Hook. species complexes).

Chambers (1963) has noted a number of anatomical differences between *C. cordifolia* and *C. nevadensis*. Further anatomical and morphological studies of *C. sibirica* s.l., *C. palustris*, and members of sect. *Rhizomatosae* are necessary before the relationship and taxonomy of these species can be clarified.

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ALLOISPERMUM INSUETUM
(ASTERACEAE: HELIANTHEAE),
A NEW SPECIES FROM COLOMBIA

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ABSTRACT

A description and illustration are provided for *Alloispermum insuetum*, a new species from Colombia.

Alloispermum Willd. (Heliantheae: Galinsoginae) includes approximately 10 species of suffrutescent shrubs and a few truly herbaceous species that occur in dry to moist mountainous regions from Mexico to northern South America. The generic name was proposed by Willdenow (1807), but not used until revived by Robinson (1978a,b, 1979). The previously undescribed species was discovered among specimens examined as part of our ongoing investigations in the subtribe.

***Alloispermum insuetum* Fernandez, Urbatsch, and Sullivan, sp. nov.**

Suffrutex, 1–2 m altus. Folia lanceolata, 5–10 cm longa. Capitulescentia ad 15 cm lata, capitulae ca. 10, pedunculis 2.5–7 cm longis. Involucra hemisphaerica, ca. 9 mm alta, 15 mm lata. Flores radii ca. 15, ligulae albae tincta apice roseae, flores disci 40–65. Achenia radii 2.5 mm longa, glabrescentia; achenia disci 2.7 mm longa, pubescentia sparsim, pappi radorum et discorum similes, squamae ca. 15, plerumque 5–5.5 mm longae (Fig. 1).

Weak, suffrutescent shrubs, 1–2 m tall. Leaves subsessile; blades lanceolate, 5–10 cm long, 2.5 cm wide, basally obtuse, apically long acuminate, abaxially pilose, with uniseriate, 5–6-celled trichomes, mainly along the veins, adaxially pubescent, with uniseriate, 2–3-celled trichomes; margins remotely serrate. Capitulescence corymbose, ca. 15 cm broad, ca. 10-headed; peduncles 2.5–7 cm long, densely pilose. Capitula 55–80-flowered; involucre hemispheric, ca. 9 mm long, ca. 15 mm wide, with phyllaries 2–3-seriate, obovate, 6.5–8.5 mm long, 4–6 mm wide, pubescent, apically acute; receptacle conical, 4.5 mm long, 4 mm wide. Ray flowers ca. 15; corollas 14–18 mm long, ligules 12–15 mm long, up to 5.5 mm wide, white with the apex tinged pinkish-red; corolla tube 2.5–4.2 mm long, densely pilose; disc flowers 40–65; corollas 6.4 mm long; ray achenes 2.5

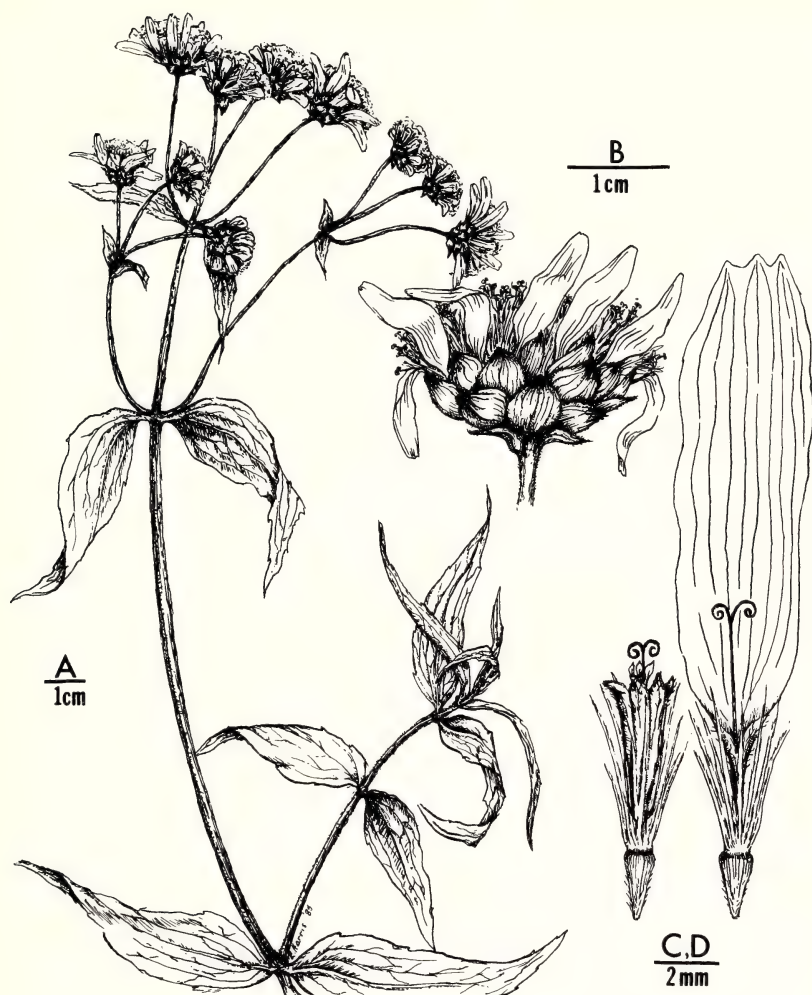


FIG. 1. *Alloispermum insuetum*. A. Habit. B. Capitulum. C. Disk flower. D. Ray flower. Drawn from *Schlim* 359.

mm long, mostly glabrous. Disc achenes 2.7 mm long, sparsely pubescent; pappus of both ray and disc achenes ca. 15 linear-lanceolate, fimbriate scales, 5–5.5 mm long.

TYPE: Colombia, Norte de Santander, Provincia de Ocaña: 8000–10,000 ft, Jan 1852, *Schlim* 359 (Holotype: K!; isotype: BM). The collection date for the type material can not be ascertained directly from the specimen label data. According to Linden (1867), Schlim explored the Ocaña region in 1851 until the beginning of 1852.

PARATYPE: Colombia, Norte de Santander, around Ocaña, *Schlim* 440 (K!).

Alloispermum insuetum is known only from the type material and one other specimen; it grows from 2400–3200 m and flowering occurs in January. This species is similar in habit, disc pappus, leaf, phyllary, and achene features to the other species in the genus. It is distinguished easily from the other South American species by its larger heads, longer ligules, and the presence of a pappus in the rays. The specific epithet “insuetum” (=unusual) was chosen to call attention to these features. *Alloispermum insuetum* is similar to larger-headed forms of *A. caracasana* (Kunth) H. Robinson, but the former has more than 40 disc flowers and about 15 ray flowers per head, whereas the latter has fewer than 35 and 8, respectively.

ACKNOWLEDGMENTS

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(Received 19 Nov 1985; revision accepted 10 Nov 1986.)

ANNOUNCEMENT

REVISED EDITION

TERRELL, E. S., S. R. HILL, J. H. WIERSEMA, and W. E. RICE, A checklist of names for 3,000 vascular plants of economic importance, Revised ed., *U.S.D.A., Agricultural Handbook*, no. 505, pp. [i–ii], 1–241, Oct. 1986, no ISBN, paper-bound, price unknown (from Superintendent of Documents, Government Printing Office, Washington, DC 20402). [First edition = 1977; a useful compilation of common names and accepted scientific names for 1241 genera and 3296 species, subspecies, and varieties, with inclusion of 983 rather common synonyms.]

A NEW SPECIES OF *AXINIPHYLLUM*
(ASTERACEAE: HELIANTHEAE) FROM
DURANGO, MEXICO

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ABSTRACT

Axiniphyllum durangense from southern Durango, Mexico, is related to *A. corymbosum* of Guerrero and adjacent Oaxaca, but is distinguished readily by its rhombic-ovate leaves and much longer outer involucre bracts.

In spite of a recent revisional treatment of the relatively small, uncommon genus *Axiniphyllum* (Turner 1978), I have observed recent collections that represent an additional novelty from southwestern Durango. This brings to five the number of species now recognized. It is noteworthy that McVaugh (1984) omitted the genus from his Flora Novo-Galiciana, but the proximity of collections of this genus to the north of Jalisco suggests that it also will be found ultimately in that floristic region.

Axiniphyllum durangense B. Turner, sp. nov.

A. corymbosum accedens sed foliis tenuioribus rhombeo-ovatis, phyllariis exterioribus multo longioribus (Fig. 1).

Erect perennial herb 50–75 cm high, arising from short, corm-like rhizomes; the root-system fibrous. Stems terete, 2–5 mm thick below; moderately to densely hirsute with crisp, spreading hairs; the upper stems less pubescent and soon beset with a dense array of short, glandular trichomes. Leaves opposite, rhombic-ovate, 5–8 cm long, 1–3 cm wide, gradually tapering into a slender petiole that abruptly flares below into a stipule-like, perfoliate appendage; blades pubescent above and below principally along the venation, 3-nerved from above the base, the margins irregularly serrulate. Heads 6–8, in an open corymbose panicle, the ultimate peduncles 1–5 cm long. Involucres hemispheric, phyllaries 2–3-seriate, the outer series of 4–6 loose, leaf-like, mostly lanceolate bracts 10–15 mm long, 1.5–2.5 mm wide; the inner series of 8–11 \pm scarious, broadly ovate bracts, 6–7 mm long, 3–4 mm wide, puberulent. Receptacle convex, ca. 2 mm across, the bracts obovate, 5–6 mm long, ca. 2 mm wide, 3–4-nerved, the apices acute. Ray florets absent. Disk florets 40–50, yellow; corollas ca. 5 mm long, the tube ca. 1 mm long, pubescent

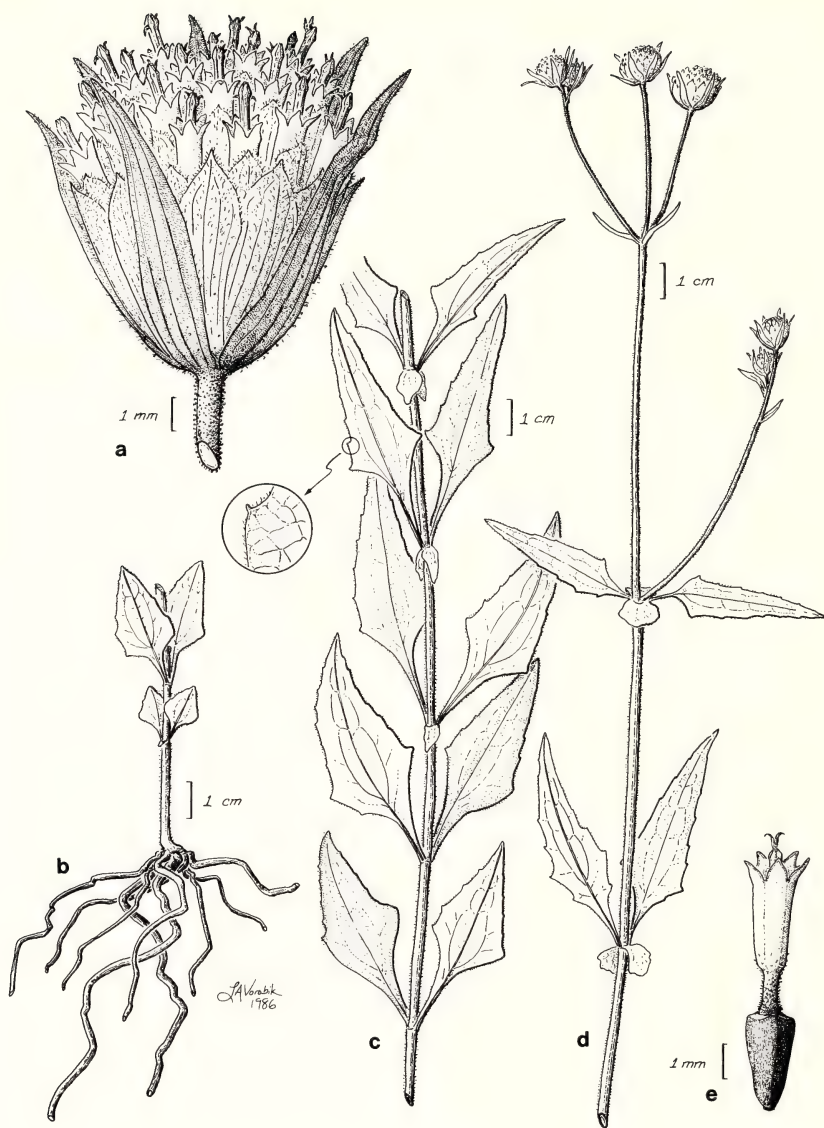


FIG. 1. *Axiniphyllum durangense* (from holotype). a. Head. b. Base of stem with roots. c. Mid-stem leaves. d. Capitulescence. e. Floret.

with both coarse hairs and short-stipulate glands, the limb ca. 4 mm long, the lobes ca. 1 mm long, acute. Anthers yellow, ca. 2.5 mm long, eglandular. Style branches hispid with abrupt conical appendages ca. 0.5 mm long. Achenes epappose, quadrate, black, smooth, 2.5–3 mm long, ca. 1 mm wide.

TYPE: Mexico, Durango, Mpio. de Mesquital: "Alrededores de Platano Tatemado (a 12 km de La Guajolota). . . . Margenes de arroyo en Bosque de pinoencino", ca. 23°30'N 104°30'W, 12 Sep 1985, *I. Solis* 294 (Holotype: TEX; isotypes: to be distributed).

PARATYPE: Durango, Mpio. Mezquital: ca. 11 km from La Guajolota, 28 Sep 1985, *Solis* 379 (TEX).

In my treatment (Turner 1978), *A. durangense* will key near *A. corymbosum*, an eradiate species of Guerrero and adjacent Oaxaca. It differs markedly from that taxon in leaf shape, vestiture and texture. In addition, the involucre bracts of *A. corymbosum* are smaller and the much narrower, outer series is only 3–5 mm long.

ACKNOWLEDGMENTS

I am grateful to Dr. M. C. Johnston for the Latin diagnosis, Dr. Linda Vorobik for providing the illustration, and especially to Dr. J. Strother for calling to my attention several glaring errors in an earlier draft of this paper.

LITERATURE CITED

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TURNER, B. L. 1978. Taxonomy of *Axiniphyllum* (Asteraceae—Heliantheae). *Madroño* 25:46–52.

(Received 25 Sep 1986; revision accepted 6 Jan 1987.)

ANNOUNCEMENT

NEW PUBLICATIONS

JENKINS, D. I., *Amanita of North America*, Mad River Press, Route 2, Box 151B, Eureka, CA 95501, 1986, vi, 198 pp., illus. (color), ISBN 0-916422-55-0 (paperbound), price unknown. [With keys to and descriptions of 128 species and varieties.]

LAMPE, K. F., and M. A. McCANN, *AMA Handbook of Poisonous and Injurious Plants*, American Medical Association, Chicago, 1985, xi, 432 pp., illus. (mostly color), ISBN 0-89970-183-3 (flexibound), \$24.95 (from Chicago Review Press, 814 North Franklin, Chicago, IL 60610). [On plants of the United States, Canada, and the Caribbean, with 437 color photographs.]

NOTES

RANGE EXTENSION, CHROMOSOME COUNT, AND MEPHITISM IN *Lessingia tenuis* (COMPOSITAE).—Recent field work in Central California revealed a range extension for *Lessingia tenuis* (A. Gray) Cov.: CA, Santa Clara Co., s. side of ridge ca. 4 airline km s. of Los Gatos, near Priest Rock and power lines along a dirt road from Lexington Reservoir to Sierra Azule Ridge, ca. 517 m, *Mooring* 3517, 3530, 3538 (UC). (fide J. Strother, UC).

First observed here in 1984, these annuals were mostly 2–3 cm tall, relatively narrow-leaved, and sparsely branched. They did not conform to descriptions (Munz, A California Fl., 1959; Abrams and Ferris, Illustr. Fl. Pacific States, 1960) nor did they closely resemble the herbarium specimens I examined. Thus, an experimental study seemed appropriate.

Achenes collected at the site and sown in vermiculite in an unheated greenhouse in November readily germinated ca. 7 days later. Twenty seedlings that were planted in pots flowered an average 175 days after germination. Mature plants were 15–23 cm tall, relatively broad-leaved, and diffusely branched, in sharp contrast to their wild parents. They matched the description of *Lessingia tenuis*, and resembled some of the herbarium specimens examined. Analysis of microsporocytes stained in acetocarmine showed in three plants that $2n = 5n$ and that meiosis was regular. This count agrees with those for populations of *L. tenuis* in San Luis Obispo and Ventura cos. [Spence, A biosystematic study of the genus *Lessingia* Cham. (Compositae), Ph.D. diss., Univ. California, Berkeley, 1963]. Stainability of fresh pollen in cotton blue-lactophenol (minimum of 300 pollen grains from each of 10 plants) ranged from 76–100% ($\bar{x} = 95\%$). Greenhouse plants differed conspicuously from wild progenitors in that each had a pungent, skunk-like odor that is unreported in this genus. Spence (pers. comm.) grew large numbers of *L. tenuis* and other species of *Lessingia*, and did not notice this odor in the genus.

The presence of *L. tenuis* in the Santa Cruz Mountains represents a 60 km westward range extension. I found the population while looking for local populations of the Western Whiptail Lizard (*Cnemidophorus tigris*), which is another example of a coastward outlier of an Inner Coast Range species (Mooring, Herp. Rev. 14:123, 1983). *Lessingia tenuis* may be a recent introduction here, from nearby power lines or road, or may have increased its numbers rapidly. I have hiked through the Los Gatos site intermittently for 20 years without seeing this species. I first noticed the Los Gatos lizard populations during the high-precipitation years associated with El Niño weather, and the discovery of *L. tenuis* came about 2 years later. The numbers, density, and distribution of the population have varied. In 1984, an estimated 500 plants occurred along ca. 150 m and within 2 m of a north-to-south trail through chaparral that is dominated by *Adenostoma fasciculatum*. In 1985 most of the ca. 150–200 individuals were within the northernmost 100 m, and also were close to the trail. In 1986, however, several thousand were scattered in clumps over 358 m, including hundreds in bare or thinly vegetated soil up to 20 m from the trail. The population was less dense in the northernmost section than it had been before, possibly due to the increased use of the trail by mountain bicycles. It has expanded southward, however, and now abuts a bulldozed area adjacent to a 1985 burn that may allow further expansion.

The skunk-like odor of the Los Gatos population should be looked for in other populations of this and other species of *Lessingia*. Presence-absence patterns might be a useful taxonomic character in a group where keys (Jepson, A Man. Fl. Plants California, 1925; Munz, op. cit.; Abrams and Ferris, op. cit.) emphasize vegetative features. Pungent mephitis in *L. tenuis* seems to be associated with relatively lux-

uriant growth, and may not be obvious in wild plants. I did not notice it when collecting and observing them in 1984. In 1986 I had to sniff the wild plants to detect it, whereas half-grown wild plants that were transplanted to the greenhouse that year were, when full-grown, almost as odorous as I remembered the 1984 greenhouse-grown seedlings to be.

Mephitis may be an anti-herbivore adaptation in the Los Gatos population of *L. tenuis*. They often occur in clumps; some occur under *Adenostoma fasciculatum*, *Arctostaphylos (glandulosa?)*, or *Baccharis pilularis* subsp. *consanguinea*. The shrubs have no surrounding bare zones unlike the situations described previously (Bartholomew, Science 170:1210–1212, 1970; Halligan, Bioscience 23:429–432, 1973). Evidence of grazing by mammals is present, but the lessingsias and co-occurring annuals [including *Navarettia squarrosa*(?), “skunkweed”] show no evidence of being grazed. The lessingsias, however, do not have an unpleasant taste (at least to me), and greenhouse plants are attacked by whiteflies. Mephitis has been reported in *Navarettia squarrosa* (see Abrams & Ferris, op. cit.) and I had noticed it in a Santa Cruz Co. population growing in a relatively mesic site. I have not observed it among local populations, however, but neither have I sniffed the plants. Perhaps mephitis, and other strong scents, might be found to be more widespread if it is looked for in greenhouse plants derived from dense populations of apparently ungrazed herbaceous species of dry habitats.

I appreciate the comments of reviewers Pinkava and Tanowitz, and have extended the discussion of mephitis.—JOHN MOORING, Biology Department, Santa Clara Univ., Santa Clara, CA 95053. (Received 25 Jun 86; revision accepted 9 Oct 1986.)

REVIEW

Vascular Plants of Upper Bidwell Park, Chico, CA. By VERNON H. OSWALD. vi + 98 pp. The Herbarium, Department of Biological Sciences, California State University, Chico, Publication No. 3. 1986. \$5.95 plus tax and mailing.

This book has an attractive sketch of *Polygonum bidwelliae* on its soft yellow cover. The content is formatted professionally and has appeal to anyone who wishes to deal with basic botany with the assistance of keys, glossary, map, and bibliography. The preface explains the three plant communities involved and has a synoptic geological presentation. The nomenclature is up-to-date and keys involve major plant groups, divisions, families, genera, species, and subspecific taxa. Although undoubtedly incomplete (as is any other new checklist), 748 species and subspecific taxa have been tabulated. About 30% of these are introduced and this is about 50% higher than on the county list.

Two thousand acres are included in the study area. Elevations extend from 260 feet to 1520 feet. Twelve plants are listed in various categories in the C.N.P.S. rare plant inventory. There is no mention of climatology and there are no illustrations or photographs. A short addenda and errata are enclosed.

Even for amateurs who have only a superficial knowledge of botany, this professionally presented text will be found more enjoyable, and certainly more educational, than a plant list keyed to the color of the flowers.—WALTER KNIGHT, Field Associate, California Academy of Sciences, San Francisco, CA 94118.

NOTEWORTHY COLLECTIONS

ARIZONA

ASTRAGALUS HYPOXYLUS S. Wats. (FABACEAE).—Santa Cruz Co., Patagonia Mts., Coronado Natl. For., ca. 4.5 km s. of Harshaw on rd. to Washington Camp, 31°26.5'N, 110°43.5'W, stony openings in pine-oak-juniper woodland, restricted to limestone-derived soil, sw. exposure, ca. 1600 m, 20 Apr 1986, *Levin and Levin 1633* (NY, RSA, SD), *T. R. and R. K. Van Devender 86-140* (ARIZ) (det. R. C. Barneby). On a subsequent visit, T. R. Van Devender (pers. comm.) found 107 plants on this hillside and a few plants ca. 1 km s.

Significance. First collections since the type collected by J. G. Lemmon (Cochise Co., Huachuca Mts., Maloney's Ranch, Jul 1882, 2656) about 30 km e. The plants are caulescent, with stems of the season up to 6 cm long, as described by Barneby (Mem. N.Y. Bot. Gard. 13:1028–1029, 1964); Kearney and Peebles (Arizona Fl., p. 469, 1951) incorrectly described the plant as acaulescent and caespitose. To Barneby's description, I add that the petals are whitish with bluish-purple tips, the banner is recurved through about 45°, and the ovules may be up to eight in number; the seeds and pod dehiscence remain unknown.—GEOFFREY A. LEVIN, see California notes below.

CALIFORNIA

FESTUCA OCCIDENTALIS Hook. (POACEAE).—San Diego Co., Palomar Mtn. State Park, Doane Valley Nature Trail ca. 250 m w. of Doane Pond, T10S R1E S5 ne.¼ of nw.¼, 1400 m, 18 Jun 1986, *Curto and Allen 330* (SD); Los Coyotes Indian Res., Hot Springs Mtn., T10S R4E S15 nw.¼ of se.¼, 1790 m, 21 Jun 1986, *D. Clemons, Levin, and Curto 1509* (SD); Santa Ysabel Indian Reserv., Volcan Mts., n. and nw. slopes of Oak Ridge, T12S R3E S12, 1585 m, 3 Jul 1986, *Curto 336* (SD); Cuyamaca Rancho State Park (CRSP), Engineers Rd. sw. of North Peak, T13S R4E, 1465 m, 3 Jun 1986, *Curto and Allen 308* (SD); CRSP, w. slope of Middle Peak, along Middle Peak Loop Fire Rd. 1 km n. of Milk Ranch, T14S R4E, 1585 m, 29 May 1986, *Curto and Allen 300* (SD, TAES, US); CRSP, Japacha Fire Rd. at Japacha Creek, T14S R4E, 1330 m, 4 Jun 1986, *Curto and Allen 310* (SD). At all sites, common in mixed conifer or pine-oak woodlands growing on loamy soils derived from gabbro or granodiorite.

Significance. A range extension of ca. 300 km se. from Santa Barbara Co. The abundance of this grass in the Peninsular Ranges of San Diego Co. indicates that it should be looked for in the intervening mountain ranges. Known previously from B.C., Canada, s. to Santa Barbara Co., CA, e. across Canada to Ont., and in ID, MT, WY, WI, and MI.—MICHAEL CURTO and LINDA ALLEN, California Dept. of Parks and Recreation, 1333 Camino del Rio S., Suite 200, San Diego, CA 92108; and GEOFFREY A. LEVIN, see notes below.

MIMULUS CONGDONII Rob. (SCROPHULARIACEAE).—San Diego Co., Cuyamaca Rancho State Park, oak woodland border n. of meadow near Merrigan Fire Rd. ca. 0.8 km n. of Viejas Blvd., 32°52'N, 116°36.75'W, 1050 m, 24 Mar 1986, *Curto 255* (SD). Several populations of about 100 plants along seasonal creeks.

Significance. A range extension of ca. 300 km se. from the Coast Ranges in Ventura Co. and ca. 350 km s. from the Greenhorn Mts., Kern Co. Known previously in the Coast Ranges from Mendocino Co. to Ventura Co. and in the Sierra Nevada from Mariposa Co. to Tulare Co.

RHUS TRILOBATA Nutt. ex Torr. & A. Gray var. *SIMPLICIFOLIA* (Greene) Barkley (ANACARDIACEAE).—San Diego Co., Piñon Peak [probably highest point in Pinyon Mts., T13S R6E S11], 24 Sep 1938, *Stover and Harbison s.n.* (SD); Vallecito Mts., T13S R6E S14 ne. $\frac{1}{4}$ of se. $\frac{1}{4}$, 1355 m, 15 May 1983, *D. Clemons and E. Jonsson 590* (SD); T13S R6E S23, 1220 m, 10 Apr 1985, *Clemons and Jonsson 1012* (SD), 1013 (SD). Apparently uncommon in pinyon-juniper woodland.

Significance. First records of this variety for CA, a n. range extension of 70 km from near La Rumorosa, Baja California Norte, Mexico. Known previously from Baja California, s. UT, n. AZ, sw. CO, and OK. Beauchamp (A fl. San Diego Co., California, p. 82, 1986) incorrectly cited the Pinyon Mts. specimen as var. *anisophylla* Jepson and he (op. cit., p. 170) used the Clemons and Jonsson specimens as the basis for listing *Ribes cereum* Dougl. in San Diego Co. The latter species remains unknown in the county.—GEOFFREY A. LEVIN, Botany Dept., San Diego Natural History Museum, P.O. Box 1390, San Diego, CA 92112.

COLORADO

BRYUM BLINDII B.S.G. (BRYOPSIDA: EUBRYA: BRYACEAE).—Grand Co., Arapahoe Natl. For., Fraser River valley at base of Berthoud Pass, T2S R75W S34, 3100 m, in saturated sand and gravel on steep slope just above roadside on e. side of lowest hairpin turn, 14 Sep 1986, *W. A. Weber & H. Dahnke 91852* (COLO; to be distributed in Krypt. Exsicc. Vindob.).

Previous knowledge. Northern and central Europe, northern Asia and Japan; rare in North America: Ontario (Thunder Bay), New Brunswick, northern Manitoba, British Columbia, and southeastern Alaska (Crum & Anderson, Mosses of Eastern North America, Vol. 1, 1981).

Significance. First record for contiguous United States.—WILLIAM A. WEBER, Univ. of Colorado Museum, Boulder 80309.

NEW MEXICO

LYGODESMIA GRANDIFLORA (Nutt.) Torr. & A. Gray (ASTERACEAE).—San Juan Co., Cutter Canyon, T29N R8W S21, silt slope, 1950 m, 9 Jun 1973, *J. T. Wynoff 492* (ASU) (det. A. S. Tomb).

Significance. First record for NM. When *L. grandiflora* was redefined (Tomb, Syst. Bot. Monogr. 1:1–51, 1980) to include only material from CO, UT, and WY, material from AZ and NM was assigned to *L. arizonica* Tomb. Recently, *L. grandiflora* s.s. was found in ne. AZ (Parfitt, J. Ariz. Nev. Acad. Sci., in press.)—BRUCE D. PARFITT, Dept. Botany, Arizona State Univ., Tempe 85287.

PENSTEMON RAMOSUS Crosswhite (SCROPHULARIACEAE).—Dona Ana Co., Sierra de las Uvas, base of Ponciello Peak, T20S R3W, 1500 m, 11 Jun 1977, *Weber s.n.* (NMC); Dona Ana Mts., sheltered ne. slopes of Summerford Mt., T21S R1E S3, 1350 m, 27 May 1984, *Todsen 8406-1* (NMC). Luna Co., ca. 1.5 km n. of Cooke's Peak, open slopes with juniper, 1800 m, T20S R8W, 17 Oct 1979, *Spellenberg, Isaacs, and Soreng 5436* (NMC). Sierra Co., arroyo e. of Rio Grande and 0.5 km s. of Caballo Dam, 1275 m, T16S R4W, 22 Jun 1986, *Todsen A119* (NMC).

Significance. Known only from the US, *P. ramosus* was previously reported from Cochise, Graham, Greenlee, and Pima cos. in se. AZ and Grant and Hidalgo cos. in NM. Above are all new county records with the Dona Ana Mts. location 180 km e. of the nearest previously reported site.—THOMAS K. TODSEN, Dept. Biol., New Mexico State Univ., Las Cruces 88003.

REVIEW

Uinta Basin Flora. By SHEREL GOODRICH and ELIZABETH NEESE. 320 p. U.S.D.A. Forest Service—Intermountain Region, Ashley National Forest and U.S.D.I. Bureau of Land Management—Vernal District. 1986.

A good local flora makes field study of plants easier. The more local, the easier, and probably better.

This is an excellent local flora. It treats an area of almost 40,000 km² that contains about 1650 species. The locale is in northeastern Utah, including the east-west trending Uinta Mts., the Uinta Basin and the adjoining Tavaputs Plateau, and a strip of adjacent Colorado about 80 km wide. Elevations range from 1288 m (4255 ft) on the Green River to 4130 m (13,528 ft) on Kings Pk. The plant communities of the area are correspondingly diverse, from cold desert and lowland riparian to alpine. Geological diversity further complicates the mosaic of habitats and plant communities. These habitats are described succinctly, accurately, and undogmatically by means of some of the plant species they contain. For individual species, habitats and abundance are described, again simply but directly. Altitudinal limits for species are given. According to the authors, the book is intended for field identification and extra keys using vegetative or fruit characters are provided often. One feature is interpolated keys that separate easily confused species such as *Carex elynoides* and *Kobresia myosuroides*. The book has a glossary, references cited, and index.

A nomogram of feet versus meters would be useful. No one outside the U.S. is going to put up with the English system of measures. We in the U.S. are stuck with altitudes in feet so long as the U.S. Geological Survey topographic maps continue their backward progress.

The U.S. Forest Service has been taking some hard knocks lately for overcutting timber, roading areas to sell timber instead of developing logging methods not requiring so many roads, foot-dragging on Wilderness classification, neglecting trails, pushing resort and helicopter skiing instead of back-country, etc. The BLM was originally set up to respond to local grazing interests, and only recently has it been able to even start an inventory of its forage resources. The Forest Service usually acts as local people want it to act. Add a Washington administration that is compulsively anti-conservationist and the public lands in the National Forests and those administered by the BLM are in deep trouble. So is the Forest Service itself. The "good guys" really need overt support when they do something that furthers good land management. Goodrich and Neese's book is just such a good thing. It is invaluable for managing vegetation, either timber or range forage, because it provides necessary help for the first question a land manager asks, What is out there? Ecological relationships can be known only when vegetation is known, and acquaintance with the flora is necessary to understand the ecology of vegetation.

The Uinta Mts. and its environs is a beautiful, rich, interesting ecosystem. This book will be a treasured aid to botanists sampling that ecosystem.—JACK MAJOR, Botany Dept., Univ. California, Davis 95616.

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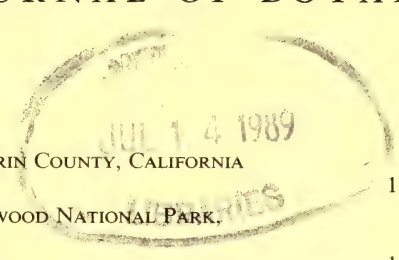
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PLANT COMMUNITIES OF RING MOUNTAIN PRESERVE, MARIN COUNTY, CALIFORNIA

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ABSTRACT

Vegetation on Ring Mountain Preserve, Marin Co., California, was sampled and plant communities were determined according to natural but dynamic boundaries. Six plant communities were identified primarily by their dominant life form: serpentine bunchgrass, mixed broadleaf evergreen forest, non-native grassland, northern coyote brush, freshwater marsh, and freshwater seep. Species composition, percent cover, and frequency of occurrence were recorded, and the percentage of the total flora and areal cover of exotic species was determined for each community. The serpentine bunchgrass community occupied the greatest areal extent and contained the smallest percentage of exotic species, both in frequency of occurrence and cover. In contrast, the non-native annual grassland community, although second in areal coverage, was dominated by exotic grasses and broad-leaved forbs. The remaining four plant communities are lesser components of the total vegetation. These vary greatly in percent cover and frequency of exotic species, which in turn are dependent on the phase of the community and the degree of past disturbance.

Ring Mountain Preserve (RMP) is an isolated remnant of the perennial bunchgrass communities that formerly characterized much of the San Francisco Bay landscape. Established by The Nature Conservancy (TNC) in 1983, the Preserve is located in southern Marin Co., California, and covers approximately 148 hectares on the summit of the Tiburon peninsula (Fig. 1). Elevation ranges from 1–200 m above sea level.

Ring Mountain is distinguished by its extensive serpentine soils that were derived from ultramafic intrusions into the widespread Franciscan sandstone formation (Taliaferro 1943). These soils tend to be thin and rocky and are accompanied by glaucophane schist outcrops. They support a highly endemic flora and are accompanied by bunchgrasses typical of deeper ultramafic soils. Seven rare plant species are found on this preserve (Smith and York 1984, Cal. Dept. Fish and Game 1986). *Calochortus tiburonensis* Hill (Tiburon mariposa) is endemic to Ring Mountain.

Although much has been written about the ultramafic soils and vegetation of California (e.g., Kruckeberg 1984), little has been published specifically on the plant communities of the Tiburon penin-

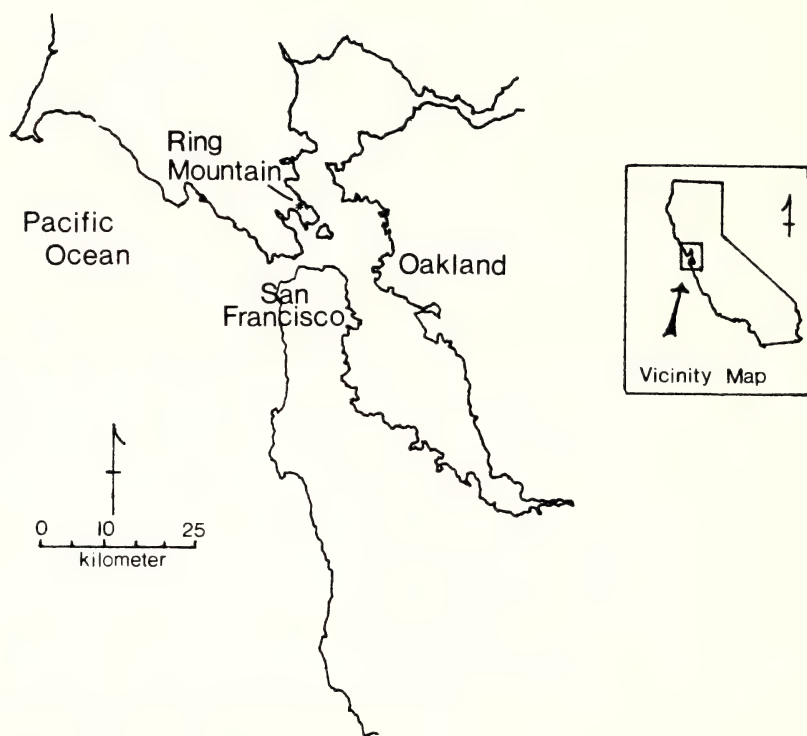


FIG. 1. Location of Ring Mountain Preserve in the San Francisco Bay area.

sula. Penalosa (1963) and Howell (1970) contain general descriptions of the major plant communities of the Tiburon peninsula and Marin Co., respectively. Certain unique features of Ring Mountain have been published (e.g., Ellman 1975), as well as general descriptions of Coastal Range vegetation types (Barbour and Major 1977).

Climate at RMP is mediterranean. Summer fog with strong winds is frequent; annual precipitation averages 71 cm, occurring mostly between November through April (Rantz 1971).

The objectives of this study were: (1) to characterize the vegetation of RMP; (2) to assess the degree of human disturbance evidenced by the percentage of exotic species that comprise each plant community; and (3) to provide data for the future management of the plant communities at the Preserve.

METHODS

Plant communities were determined using the California natural community classification system of the Natural Diversity Data Base

(Jensen and Holstein 1983). This vegetation classification, a recent improvement on the more widely used system of Cheatham and Haller (1975), was used because of its wide acceptance and usage by TNC and public organizations. The terms plant community and vegetation type are used interchangeably throughout the text, and one term is not used preferably over the other.

Plant communities were mapped for RMP from March through July 1983 from aerial photographs taken the same spring. These communities were delineated first on acetate overlays on aerial contact and composite photographs, and then verified in the field. Areal extent of each community was determined with a Lasico compensating polar planimeter (Series 40). Samples of each unit were located randomly on a working map for study in the field.

Each community was sampled from March through May 1984 and April 1986. As a result of an early spring sampling period, some conspicuous species that flower later in the spring and summer (e.g., *Danthonia californica*) were not recorded. Species composition, ground slope, aspect, and topographic position were obtained for each community. For the serpentine bunchgrass, non-native grassland, freshwater marsh, and freshwater seep communities, a standard 1% areal sample was achieved, using the point intercept method (Mueller-Dombois and Ellenberg 1974). Sampling transects were run along slope contours from randomly chosen points along a line-transect that was oriented perpendicular to the contours. The northern coyote brush community was sampled by the line-intercept method (Canfield 1941) to achieve a 5% sample of the total area.

Random points were located within a random sample of the mixed broadleaf evergreen forest, and data were obtained by the point-centered quarter method (Mueller-Dombois and Ellenberg 1974). A 5% areal sample was attained for this community. At each point, data on tree and sapling composition, shrub species composition, and percent cover were estimated on four 25 m² subplots. For herb species, percent cover was estimated on four 5 m² plots at each tree subplot. Botanical nomenclature follows that of Munz (1968) with only a few exceptions.

After field sampling, the serpentine bunchgrassland, non-native grassland, northern coyote brush, and mixed broadleaf evergreen forest communities were divided into 'phases' according to aspect, topographic position, ground slope, and canopy layer and represent variations within community types.

Percent exotic species within the flora of each community and percent total plant cover by exotic species for each community were computed and tested with a chi-square statistic with a continuity correction (Grieg-Smith 1983). This test determined whether any significant differences in the extent of exotic species within the various phases of each vegetation type occurred. The Jaccard Index was

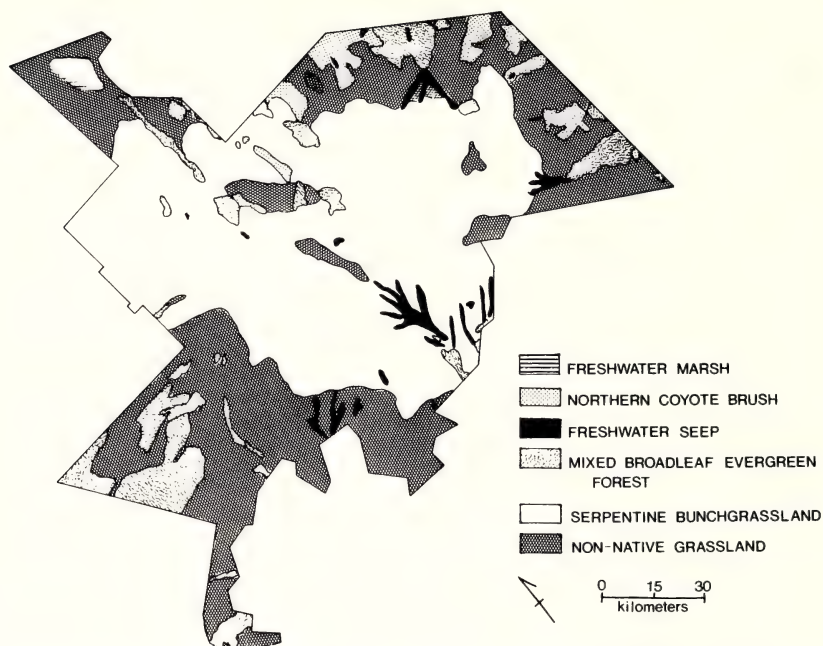


FIG. 2. Distribution of the six plants communities on Ring Mountain Preserve.

computed to examine the floristic similarities among communities (Grieg-Smith 1983).

RESULTS

Six communities were identified on RMP: serpentine bunchgrass (SBG), non-native (annual) grassland (NNG), mixed broadleaf evergreen forest (MBEF), northern coyote brush (NCB), freshwater marsh (FWM), and freshwater seep (FWS) (Fig. 2). The SBG community is the dominant vegetation type, representing 70 ha (47% of the total area). NNG is slightly less extensive on RMP, comprising 49 ha (33%) that are primarily on the lower slopes.

MBEF covers approximately 16 ha (11%) that occur in irregularly scattered stands throughout the Preserve. The FWM, FWS, and NCB communities are of much smaller distribution. These represent 1.4 ha (<1%), 4.7 ha (3%), and 7.3 ha (5%) of RMP, respectively.

Serpentine bunchgrass. This community occurred most frequently on the upper slopes and ridgetops (Fig. 3). Ground slope varied from zero at the upper elevations to greater than 25% at midslope. Fifty-six species that represent a predominately native flora were recorded in this plant community (Table 1). The exotic *Lolium multiflorum*



FIG. 3. Serpentine bunchgrass community type, which is typified by many boulders strewn among various perennial grasses and bulbous plant species.

Lamk. and the ubiquitous native *Chlorogalum pomeridianum* (DC.) Kunth were the species most frequently encountered. Perennial bunchgrasses, particularly *Stipa pulchra* Hitchc. and *Melica torreyana* Scribn., also were abundant. A high frequency (14%) of exposed bedrock and boulders typified this vegetation type on RMP.

The richness of the flora is shown by the low frequency of occurrence of most herbs. A little greater than 71% (40 species) of the flora occurred less than 1% of the time, whereas no species occurred more frequently than 13%. Infrequent species were represented by both annual and perennial native forbs.

All seven rare species on RMP were found in this community, but only those most abundant in the early and mid-spring were recorded during this sampling period. These species are: *Calochortus tiburonensis* Hill, *C. umbellatus* Wood, *Castilleja neglecta* Zeile, *Calamagrostis ophitidis* (J. T. Howell) Nygren, *Eriogonum caninum* (Greene) Munz, *Hesperolinon congestum* (Gray) Small, and *Hemizonia congesta* DC. subsp. *vernalis* Keck. Of these, *Calamagrostis ophitidis* is most frequently encountered. *Eriogonum caninum* was localized throughout the Preserve, and not represented in the sample. *Hesperolinon congestum* also was not recorded. Although widespread, it is rarely abundant locally.

Mixed broadleaf evergreen forest. This community was found in the most mesic habitats on RMP. These include the drainages near groundwater seeps (Fig. 4), and the large rock outcrops (Fig. 5). Species composition in these two habitats were similar, and, thus, MBEF was treated as a relatively homogeneous plant community that is characterized by three canopy layers.

TABLE 1. PERCENT FREQUENCY OF OCCURRENCE FOR EACH SPECIES RECORDED IN THE SERPENTINE BUNCHGRASSLAND, NON-NATIVE GRASSLAND, MIXED BROADLEAF EVERGREEN FOREST, FRESHWATER MARSH, AND FRESHWATER SEEP, AND PERCENT COVER FOR EACH SPECIES RECORDED IN THE NORTHERN COYOTE BRUSH ON RING MOUNTAIN PRESERVE. SBG = serpentine bunchgrassland; NNG = non-native grassland; NCB = northern coyote brush; FWM = freshwater marsh; FWS = freshwater seep; MBEF = mixed broadleaf evergreen forest.

PART I: SBG and NNG				SBG frequency (%)			NNG frequency (%)		
Species	N-slope	S-slope	Ridgetop	Total	N-slope	S-slope	Total	N-slope	S-slope
<i>Lolium multiflorum</i>	9.98	22.65	9.66	12.46	—	27.32	21.18	—	—
<i>Stipa pulchra</i>	10.98	11.47	8.24	9.91	3.08	7.45	5.42	—	—
<i>Chlorogalum pomeridianum</i>	6.82	12.65	10.28	9.48	—	1.16	0.84	—	—
<i>Melica torreyana</i>	6.32	5.00	6.53	6.14	—	—	—	—	—
<i>Avena</i> spp.	3.66	1.76	8.66	5.41	1.76	4.97	3.61	—	—
<i>Achillea borealis</i> subsp. <i>californica</i>	4.33	2.35	5.97	4.62	2.64	0.33	0.96	—	—
<i>Vulpia dertonensis</i>	2.49	1.47	6.39	3.95	3.96	2.48	2.89	—	—
<i>Lasthenia californica</i>	4.49	0.59	1.99	3.10	—	—	—	—	—
<i>Calamagrostis ophitidis</i>	5.82	—	1.14	2.61	—	—	—	—	—
<i>Holcus lanatus</i>	1.83	3.53	1.28	1.95	—	—	—	—	—
<i>Dichlostenma pulchella</i>	3.33	1.47	0.85	1.88	—	—	—	—	—
<i>Eschscholzia californica</i>	1.00	1.76	2.41	1.76	—	0.16	0.13	—	—
<i>Melica californica</i>	2.99	2.35	0.28	1.70	0.44	0.16	0.25	—	—
<i>Elymus triticoides</i>	3.99	—	—	1.46	6.61	—	—	—	—
<i>Stipa lepida</i>	2.00	0.88	0.99	1.34	—	0.33	0.24	—	—
<i>Trifolium albopurpureum</i>	1.33	—	1.99	1.34	—	—	—	—	—
<i>Calochortus tiburonensis</i>	1.33	0.29	1.56	1.22	—	—	—	—	—
<i>Linanthus androsaceus</i>	1.33	—	1.14	0.97	—	—	—	—	—
<i>Phacelia californica</i>	0.83	1.18	1.56	0.91	—	—	—	—	—
<i>Sanicula tuberosa</i>	0.83	0.59	1.14	0.91	—	—	—	—	—
<i>Eriogonum nudum</i>	0.83	0.59	0.99	0.85	—	—	—	—	—
<i>Sanicula bipinnatifida</i>	1.33	0.29	0.57	0.79	—	—	—	—	—
<i>Sitanion jubatum</i>	1.66	—	0.42	0.79	—	—	—	—	—
<i>Calystegia subcaulis</i>	0.33	—	1.42	0.73	0.44	—	—	—	—
<i>Orthocarpus densiflorus</i>	0.83	—	0.85	0.69	—	—	—	—	—
<i>Sisyrinchium bellum</i>	1.33	0.88	—	0.69	—	—	—	—	—

TABLE 1. CONTINUED.

PART I: SBG and NNG Species	SBG frequency (%)			NNG frequency (%)		
	N-slope	S-slope	Ridgetop	Total	N-slope	S-slope
Unidentified Asteraceae	1.00	0.59	0.42	0.69	—	0.16
<i>Hemizonia congesta</i> ssp. <i>vernalis</i>	1.50	—	0.14	0.61	—	—
<i>Convolvulus arvensis</i>	—	1.76	0.14	0.43	—	—
<i>Elymus glaucus</i>	0.50	—	0.42	0.36	—	—
Unidentified dicotyledon seedling	0.33	0.88	0.14	0.36	0.44	0.33
<i>Lotus humistratus</i>	0.17	—	0.71	0.36	—	—
<i>Ranunculus californicus</i>	0.83	—	0.14	0.36	0.44	0.13
<i>Galium nuttallii</i>	0.17	—	0.57	0.30	—	—
<i>Geranium molle</i>	0.66	—	0.71	0.30	—	—
<i>Lomatium dasycarpum</i>	0.33	0.29	0.28	0.30	—	—
<i>Plantago hookeriana</i> var. <i>californica</i>	0.33	0.88	0.42	0.30	1.76	0.16
<i>Euphorbia spathulata</i>	—	0.29	0.42	0.25	—	—
<i>Plantago lanceolata</i>	—	—	0.57	0.25	16.30	5.30
<i>Dudleya farinosa</i>	0.33	—	0.28	0.24	—	—
<i>Layia platyglossa</i>	—	1.18	—	0.24	—	—
<i>Mentha pulegium</i>	0.33	—	0.28	0.24	0.44	—
<i>Microseris douglasii</i>	—	1.18	—	0.24	—	0.53
<i>Plantstemon californica</i>	0.66	—	—	0.24	—	—
<i>Montia perfoliata</i>	0.33	—	0.14	0.18	—	—
<i>Bromus carinatus</i>	—	0.59	—	0.12	—	—
<i>Bromus mollis</i>	—	0.59	—	0.12	1.76	1.66
<i>Castilleja neglecta</i>	0.33	—	—	0.12	—	—
<i>Dodecatheon hendersonii</i>	0.33	—	—	0.12	—	—
<i>Juncus occidentalis</i>	0.33	—	—	0.12	—	—
<i>Orthocarpus attenuatus</i>	—	—	0.28	0.12	—	—
<i>Polypodium californicum</i>	—	—	0.28	0.12	—	—
<i>Calystegia purpuratus</i>	—	—	0.14	<0.10	—	—
<i>Geranium dissectum</i>	0.17	—	—	<0.10	—	1.16
<i>Orthocarpus castillejeoides</i>	—	—	0.17	<0.10	—	—

TABLE I. CONTINUED.

PART I: SBG and NNG Species	SBG frequency (%)			NNG frequency (%)		
	N-slope	S-slope	Ridgetop	Total	N-slope	S-slope
<i>Pityrogramma triangularis</i>	—	—	0.17	<0.10	—	—
<i>Trifolium microdon</i>	—	—	0.14	<0.10	—	—
Bare soil	1.00	0.59	0.42	0.67	0.88	0.16
Bedrock/boulders	8.82	19.12	16.48	14.22	0.44	0.16
<i>Briza maxima</i>	—	—	—	—	1.76	29.16
<i>Carduus pycnocephalus</i>	—	—	—	—	—	9.27
<i>Cynodon dactylon</i>	—	—	—	—	20.70	0.83
<i>Grindelia hirsutula</i>	—	—	—	—	7.05	2.32
<i>Gastridium ventricosum</i>	—	—	—	—	11.45	0.16
<i>Bromus diandrus</i>	—	—	—	—	—	4.30
<i>Pteridium aquilinum</i> var. <i>pubescens</i>	—	—	—	—	5.29	1.66
<i>Erodium botrys</i>	—	—	—	—	0.88	2.98
<i>Calochortus umbellatus</i>	—	—	—	—	2.20	1.66
<i>Aira caryophyllea</i>	—	—	—	—	—	1.99
<i>Juncus patens</i>	—	—	—	—	3.08	0.33
<i>Iris douglasiana</i> var. <i>major</i>	—	—	—	—	1.03	0.66
<i>Juncus tenuis</i> var. <i>congestus</i>	—	—	—	—	1.76	0.33
<i>Foeniculum vulgare</i>	—	—	—	—	—	0.99
<i>Rumex acetosella</i>	—	—	—	—	—	0.83
<i>Briza minor</i>	—	—	—	—	—	0.66
<i>Wyethia angustifolia</i>	—	—	—	—	0.44	0.50
<i>Hordeum leporinum</i>	—	—	—	—	—	0.50
<i>Lupinus succulentus</i>	—	—	—	—	0.44	0.50
<i>Baccharis pilularis</i> subsp. <i>consanguinea</i>	—	—	—	—	0.88	—
<i>Silybum marianum</i>	—	—	—	—	0.44	0.16
<i>Zigadenus fremontii</i>	—	—	—	—	0.88	—
<i>Anagallis arvensis</i>	—	—	—	—	—	0.16
<i>Mentha pulegium</i>	—	—	—	—	0.44	—
						0.13

TABLE 1. CONTINUED.

PART II: NCB, FWM, FWS, MBEF Species	NCB cover (%)			Frequency (%)		MBEF frequency (%)		
	Upper	Mid	Lower	Total	FWM	FWS	Tree	Shrub
<i>Lolium multiflorum</i>	—	—	—	—	—	1.23	—	—
<i>Chlorogalum pomeridianum</i>	0.56	3.71	6.62	3.30	—	6.79	—	—
<i>Avena</i> spp.	—	—	—	—	—	—	—	—
<i>Achillea borealis</i> subsp. <i>californica</i>	—	—	—	—	—	1.23	—	—
<i>Vulpia dertonensis</i>	—	—	—	—	—	0.62	—	—
<i>Dichloctemma pulchella</i>	—	—	—	—	—	1.85	—	—
<i>Melica californica</i>	2.07	—	—	0.89	—	—	—	—
<i>Elymus triticoides</i>	1.90	4.70	0.36	2.08	0.22	0.34	—	—
<i>Elymus glaucus</i>	—	—	—	—	—	—	—	5.26
<i>Ranunculus californicus</i>	—	—	—	—	—	6.79	—	10.52
<i>Plantago lanceolata</i>	—	—	—	—	—	—	—	5.26
<i>Bromus mollis</i>	—	—	—	—	—	3.09	—	—
<i>Juncus occidentalis</i>	—	—	—	—	5.31	—	—	—
Bedrock/boulders	—	—	—	—	—	7.41	—	—
<i>Briza maxima</i>	—	—	1.27	0.42	—	—	—	10.52
<i>Carduus pycnocephalus</i>	—	3.46	1.45	1.31	1.33	1.23	—	—
<i>Cynodon dactylon</i>	—	—	—	—	—	3.70	—	—
<i>Gastroidium ventricosum</i>	—	—	—	—	—	—	—	5.26
<i>Pteridium aquilinum</i> var. <i>pubescens</i>	—	—	—	—	—	—	—	5.26
<i>Juncus patens</i>	—	—	—	—	0.22	0.62	—	—
<i>Iris douglasiana</i> var. <i>major</i>	—	—	—	—	—	—	—	10.52
<i>Rumex acetosella</i>	—	0.25	0.18	0.12	4.65	—	—	—
<i>Baccharis pilularis</i> subsp. <i>consanguinea</i>	55.86	40.59	48.78	49.75	—	2.47	—	—
<i>Silybum marianum</i>	—	0.49	4.71	1.55	1.77	—	—	—
Non-native grassland	31.03	44.80	34.27	35.41	—	—	—	—
<i>Thermopsis macrophylla</i>	4.12	0.99	1.27	2.44	—	1.23	—	—
<i>Oemleria cerasiformis</i>	3.03	—	—	1.31	—	—	—	—

TABLE 1. CONTINUED.

PART II: NCB, FWM, FWS, MBEF Species	NCB cover (%)			Total	Frequency (%)		MBEF frequency (%)		
	Upper	Mid	Lower		FWM	FWS	Tree	Shrub	Herb
<i>Toxicodendron diversiloba</i>	2.21	—	—	0.95	—	—	—	100.00	—
<i>Symphoricarpos rivularis</i>	0.56	—	0.36	0.36	—	—	—	52.63	—
<i>Picris echioides</i>	—	0.49	—	0.12	2.43	—	—	—	—
<i>Stachys rigida</i> var. <i>quercetorum</i>	—	0.49	—	0.12	—	—	—	—	10.52
<i>Heteromeles arbutifolia</i>	<0.01	—	—	<0.01	—	—	—	—	—
<i>Oenothera ovata</i>	—	—	0.18	<0.01	—	—	—	—	5.26
<i>Rosa californica</i>	<0.01	—	—	<0.01	—	—	—	—	—
<i>Festuca arundinacea</i>	—	—	—	—	25.88	—	—	—	—
<i>Carex densa</i>	—	—	—	—	16.81	—	—	—	—
<i>Juncus phaeocephalus</i> var. <i>paniculatus</i>	—	—	—	—	13.50	—	—	—	—
<i>Luzula comosa</i>	—	—	—	—	—	15.43	—	—	—
<i>Carex serratodens</i>	—	—	—	—	2.65	—	—	—	—
<i>Carex amplifolia</i>	—	—	—	—	—	12.96	—	—	—
<i>Carex tumulicola</i>	—	—	—	—	—	14.61	—	—	—
<i>Juncus bufonius</i>	—	—	—	—	2.43	—	—	—	—
<i>Perideridia kelloggii</i>	—	—	—	—	—	4.94	—	—	—
<i>Carex praegracilis</i>	—	—	—	—	1.33	4.94	—	—	—
<i>Polypogon monspeliensis</i>	—	—	—	—	—	6.17	—	—	—
<i>Juncus effusus</i> var. <i>pacificus</i>	—	—	—	—	1.11	4.94	—	—	—
<i>Rumex crispus</i>	—	—	—	—	—	1.85	—	—	—
<i>Dipsacus fullonum</i>	—	—	—	—	0.44	—	—	—	—
<i>Stachys pycnantha</i>	—	—	—	—	0.44	0.68	—	—	—
<i>Erodium cicutarium</i>	—	—	—	—	0.22	0.34	—	—	—
<i>Galium aparine</i>	—	—	—	—	—	1.23	—	—	31.58
<i>Mimulus aurantiacus</i>	—	—	—	—	—	0.62	—	—	—
<i>Lilaea scilloides</i>	—	—	—	—	—	1.23	—	—	—
<i>Vulpia</i> sp.	—	—	—	—	—	0.62	—	—	—



FIG. 4. Mixed broadleaf evergreen forest community, drainage phase. Note the linear aspect of this type. Darker regions in the grasslands are the freshwater seeps.

A small grove of eucalyptus (*Eucalyptus globulus* Labill.) was found on the west-southwest arm of RMP, and is mapped as part of the MBEF community. *Eucalyptus* is not considered a natural plant community (Jensen and Holstein 1983), represents only a small portion of the preserve, and was omitted from the sample.

The tree layer of MBEF contains four species: *Quercus agrifolia* Nee, *Lithocarpus densiflora* (H. & A.) Rehd., *Umbellularia californica* (H. & A.) Nutt., and *Arbutus menziesii* Pursh (Table 1). The latter two species occurred slightly less frequently (26.3% and 10.5%, respectively) than the former two (31.6% and 31.6%, respectively). Other tree species typical of the mixed broadleaf evergreen forest



FIG. 5. Mixed broadleaf evergreen forest, rock outcrop phase, surrounding large, often exposed boulders, and typically found on the upper slopes of Ring Mountain.



FIG. 6. Northern coyote brush community, found above the broadleaf evergreen forests, on the lower slopes of the Preserve and adjacent urban areas.

(cf. Sawyer et al. 1977), such as *Aesculus californica* (Spach) Nutt., are infrequent on RMP, and were not recorded in this sample.

Sapling frequency differed from that of tree frequency. *Umbellularia californica* was the most frequent tree species as a sapling (52.6%), whereas the remaining tree species were at a lower frequency as saplings (*Q. agrifolia* 15.8%; *L. densiflora* 21.1%). *Arbutus menziesii* was absent from the understory as a sapling.

The shrub layer of MBEF was more species rich than its overstory. Those species found in this layer include: *Corylus cornuta* Marsh. var. *californica* (A. DC.) Sharp, *Physocarpus capitatus* (Pursh) Ktze., *Pteridium aquilinum* (L.) Kuhn var. *pubescens* Underw., *Rhamnus californica* Esch., *Rubus ursinus* C. & S., *Symphoricarpos rivularis* Suksd., and *Toxicodendron diversiloba* Greene (Table 1). *Toxicodendron diversiloba* was a common understory species (100% frequency) and represented 19% of the total understory shrub cover. *Corylus cornuta* var. *californica* was less frequently encountered (16%), and its mean cover was slightly less than 14%. Conversely, *S. rivularis* was common in the understory (52%), but its average cover was typically low (8%). The remaining four species were both sparse in coverage and infrequent in occurrence (Table 1).

The herb layer of this community was more species rich than either the tree or shrub layers. Weedy species characteristic of a variety of habitats have invaded this herbaceous layer. Eighteen herb species were recorded in the MBEF flora. *Avena* spp. showed the highest mean cover (37%). Eighty-three percent of the species showed less than 1% areal cover and reflected the openness of this stratum. The range in frequency of occurrence for most herbs was 5–10% (Table 1).



FIG. 7. Non-native annual grassland lacks obvious rock outcrops and is characterized by the smooth texture of the grassland slopes. Note coyote brush and mixed broadleaf evergreen forest in the drainage at center.

Northern coyote brush. The NCB community was found primarily along the lower to middle slopes of RMP, although it also occurred at the higher elevations within the eastern boundaries of the Preserve (Fig. 6). This community was found typically on slopes that ranged from 20–30%. *Baccharis pilularis* DC. subsp. *consanguinea* (DC.) C. B. Wolf comprises between 41–59% of the total cover, depending on the slope location (Table 1). Within this shrub community, the NNG community occupied slightly less of the total cover (31–45%). The remaining species recorded in this vegetation type are largely broad-leaved forbs (e.g., *Chlorogalum pomeridianum*, *Carduus pycnocephalus* L.) that are distinctive, locally abundant members of the grassland communities. Additional shrub species (e.g., *Thermopsis macrophylla* H. & A., *Toxicodendron diversiloba*, and *Rosa californica* C. & S.), were recorded occasionally, and do not represent a significant component of the community.

With the exception of *C. pomeridianum*, there were few elements typical of the serpentine bunchgrass community in this vegetation type. Those that were found (e.g., *Melica californica* Scribn.) occur in sparse amounts in the *Baccharis* scrub and only on the upper slopes of RMP.

Freshwater seep. The FWS community lines many of the ephemeral drainages, mostly on the southern portion of RMP (Fig. 4). This vegetation type is characterized by the presence of surface water, although some drainages typically dry completely by June.

Carex densa Bailey and *Juncus phaeocephalus* Engelm. var. *paniculatus* Engelm. were the most frequently encountered species in the freshwater seeps. No species occurred more frequently than 20%. Some exotic grasses such as *Polypogon monspeliensis* (L.) Desf.,



FIG. 8. Freshwater marsh is characterized by the light-colored, exotic grass *Festuca arundinacea* in the center and by the ring of dark-colored, native species.

Cynodon dactylon (L.) Pers., and *Cortaderia selloana* (Schult.) Asch. & Graebn., have established extensively throughout these seep areas.

Non-native grassland. NNG is the second largest plant community in areal extent (Fig. 7). This grassland was found on all aspects, with ground slope varying from less than 5% to nearly 25%. South- and north-facing slopes appeared different with respect to species composition (Table 1). For example, southern slopes of the non-native grassland had a relatively high concentration of exotic weedy species [e.g., *Carduus pycnocephalus* (9.27%); *Bromus diandrus* Roth. (4.30%); *Briza maxima* L. (29.16%); *Silybum marianum* (L.) Gaertn. (0.16%)], whereas the northern slopes still harbored remnants of the SBG community [e.g., *Stipa pulchra* (3.08%); *Melica californica* (0.44%); *Calochortus umbellatus* (2.20%)].

Of the 43 plant species recorded for this grassland, more species exhibited higher frequencies of occurrence than in SBG. For example, in NNG we recorded a 20% frequency for *Briza maxima* and *Lolium multiflorum* (Table 1). By contrast, the most abundant species in the native SBG community was *Lolium multiflorum* at 13%. Both grasslands had an approximately equal portion of the flora exhibiting less than 1% frequency of occurrence (67% for NNG; 70% for SBG). The NNG community, however, is extremely variable throughout the preserve, and is difficult to characterize generally.

Freshwater marsh. This community occurs at the northern entrance to the Preserve (Fig. 8). It is a permanent wetland of less than 5% slope, and historically may have been of brackish or saltwater origin (Josselyn, pers. comm.). It is now separated from an adjacent tidal marsh by a road.

TABLE 2. MATRIX OF THE JACCARD COEFFICIENT OF SIMILARITY FOR THE SIX PLANT COMMUNITIES OF RING MOUNTAIN PRESERVE. SBG = serpentine bunchgrass; NNG = non-native grassland; MBEF = mixed broadleaf evergreen forest; NCB = northern coyote brush; FWM = freshwater marsh; FWS = freshwater seep.

	SBG	NNG	MBEF	NCB	FWM	FWS
SBG	—	24.69	6.17	4.23	1.37	9.59
NNG	—	—	12.31	15.09	7.02	15.52
MBEF	—	—	—	15.00	0.00	5.77
NCB	—	—	—	—	11.11	13.33
FWM	—	—	—	—	—	5.26
FWS	—	—	—	—	—	—

The freshwater marsh was dominated by the exotic *Festuca arundinacea* (26%; Table 1), whereas the marsh periphery was surrounded by a variety of freshwater plants (e.g., *Carex* spp., *Typha angustifolia* L.; Table 1) that occurred less commonly. Several ubiquitous exotic species (e.g., *Rumex acetosella* L., *Picris echioides* L.) occurred frequently in this community (Table 1).

Community similarities. A simple measure of floristic similarity among the five plant communities on RMP was computed using Jaccard's coefficient of similarity (Grieg-Smith 1983; Table 2). In general, overall similarities are moderate.

The two grassland communities, SBG and NNG, exhibited the greatest similarity among all the plant communities present on RMP. The SBG community, however, did not share many species with any of the other plant communities. NCB was most similar to MBEF and NNG, two communities with which it interdigitates. NNG also showed similar floristic affinities with FWS, the plant community typically found in the wetter portions of this exotic grassland. MBEF did not appear to share many species with the other vegetation types other than NNG. Finally, FWM showed little floristic affinity to any of the other plant communities on RMP.

Exotic species. Percent total number of species and total cover of each plant community was tested to determine whether the different phases of each type differed significantly. The percentage of exotic flora differed greatly among the six plant communities (Table 3).

Less than 14% of the total flora of the SBG community was exotic, whereas NNG possessed 44% exotic species. The NCB, MBEF, and FWM communities possessed 32%, 33%, and 41% exotic species, respectively (Table 3).

The NCB community differed significantly among its phases in percentage of exotic flora. The upper slope possessed 9% exotic species, midslope 50%, and the lower slope 38%. All slope sections were significantly different from each other (Table 3).

MBEF also showed a significant difference in percentage of exotic

TABLE 3. PERCENT OF TOTAL FLORA AND COVER OF EXOTIC SPECIES FOR EACH PLANT COMMUNITY AT RING MOUNTAIN PRESERVE. * = $p < 0.05$; ** = $p < 0.01$; χ^2 = chi-square statistic with a continuity correction.

Plant community	No. exotic species	% flora exotic	% cover exotic	χ^2 (flora)	χ^2 (cover)
Serpentine bunchgrass					
North slope (N)	6	12.50	2.76	N vs. S 0.4033	N vs. S 2.4061
South slope (S)	5	16.67	8.90	S vs. R 0.0076	S vs. R 2.1141
Ridgetop (R)	7	15.22	3.03	N vs. R 0.1239	N vs. R 0.0948
Total	8	13.79	1.26	—	—
Non-native grassland					
North slope (N)	9	32.14	55.50	N vs. S 2.7020	N vs. S 18.8316**
South slope (S)	16	44.44	84.60	—	—
Total	19	44.19	80.30	—	—
Mixed broadleaf evergreen forest					
Tree layer (T)	0	0.00	0.00	T vs. S —	T vs. S —
Shrub layer (S)	0	0.00	0.00	S vs. H 37.6313**	S vs. H 85.3261**
Herb layer (H)	6	33.33	61.20	T vs. H 37.6313**	T vs. H 85.3261**
Total	6	33.33	61.20	—	—
Northern coyote brush					
Upper slope (U)	1	9.11	31.03	U vs. M 38.2135**	U vs. M 6.3445*
Midslope (M)	5	50.11	49.50	M vs. L 2.2346**	M vs. L 0.8777
Lower slope (L)	5	38.50	41.90	L vs. U 22.2181**	L vs. U 2.1024
Total	6	31.60	38.90	—	—
Freshwater marsh	7	41.18	45.73	—	—
Freshwater seep	6	26.09	14.05	—	—

flora between the herb and shrub layers, and between the herb and tree layers. These differences were the result of an entirely native tree and shrub layer, and an herb layer with a rather high component of exotic species. Finally, neither of the other two communities tested (SBG, NNG) differed significantly between community phases with respect to percent of exotic flora.

When the plant communities were analyzed according to the percentage of the total cover occupied by exotic species, a different pattern emerged. NCB showed no differences between cover occu-

pied by exotics among the three slope positions, whereas the north and south exposures of NNG were significantly different. The southern slopes of this grassland had a much greater cover by exotics than the northern slope (84% and 55%, respectively; Table 3). As expected, in MBEF, the herb layer in this community had significantly greater cover by exotic species than either the shrub or tree layer.

DISCUSSION

The flora of ultramafic soils has been a perennial source of interest to California botanists. The literature concerning ultramafic communities in California recently has been summarized by Kruckeberg (1984). He suggested that the San Francisco Bay region does not harbor unusual range extensions of ultramafic species. We have found that the flora of RMP provides no exceptions.

The SBG community of RMP is a diverse, native, perennial grassland that is important because of its rather undisturbed condition in which seven rare plant species occur. In an areal context, the native SBG type remains the dominant plant community on the Preserve. The small percentage of exotic species in this community, both with respect to percent frequency of occurrence and cover, contrasts sharply with the adjacent NNG community.

The NNG community harbors certain bunchgrass species of SBG, such as *Stipa pulchra* and *Melica californica*, but it remains dominated by opportunistic exotic grasses and broad-leaved forbs. Certain areas, such as the colluvial soils and shaded portions of this community, are dominated by *Lolium multiflorum*, a grass that presumably was seeded when Ring Mountain was managed privately for grazing by dairy cattle during the 1950's (Lozier, pers. comm.). Although the variability of this grassland is extensive, the dominant species (*L. multiflorum*, *Briza maxima*, and *Plantago lanceolata* L.) are predictably the same for the two slope phases. On RMP, the NNG community most clearly reflects the mountain's recent land use history of cattle grazing, fire suppression, and off-road vehicular use.

MBEF represents a smaller portion of the RMP flora, and will likely remain so because of its restriction to the drainages and larger rock outcrops. Species composition of the tree and shrub portions of this community is typical of the mixed evergreen forests throughout the North Coast Ranges of California (Sawyer et al. 1977). The herbaceous stratum, however, consists largely of exotic species.

The FWS community is significant in that it reflects the complex geology of Ring Mountain, where ultramafic intrusion, shearing, and orogenic activities have created a complex soil and bedrock profile. Typical freshwater plants are found in the seeps and areas where ground water is not visible, but is present immediately below the

soil surface. Several of the seeps have been disturbed greatly by cattle grazing and more recently by off-road vehicular traffic. We suggest that the high proportion of exotic species in this community is the result of such long-term disturbances.

FWM contains a flora that is distinctive compared with the remaining preserve. This marsh, historically a brackish wetland bordering San Francisco Bay, is no longer influenced by tidal cycles. Therefore, under present hydrologic conditions, it is expected that this community will maintain a flora of exotic and native species typical of disturbed freshwater marshes.

NCB may be a recently established plant community in the study area. Its probable origin lies in the cessation of grazing by cattle and of fires set by Native Americans (Lewis 1973). We have observed this as a mid-successional sere that is invading NNG. Extensive areas of NNG interdigitating with NCB support the observation that *B. pilularis* subsp. *consanguinea* is invading and changing the composition of the NNG community. *Baccharis* cover is rarely greater than 50% cover anywhere along the hillsides. Under existing conditions, i.e., the absence of fire and grazing, percent cover of coyote brush is likely to increase on the lower slopes.

The importance of RMP lies not only in its distinctive floristic composition, but also in the relatively pristine condition of the SBG community. The Preserve's flora, however, reflects both its unusual geology and its history of cattle grazing, fire suppression, and other recent forms of site disturbance. Management of this preserve will require baseline information as provided in this community study. Finally, periodic monitoring to record changes in the structure and composition of the vegetation will provide information to support future management decisions.

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ANNOUNCEMENT

NEW PUBLICATIONS

BOWERS, J. E., A career of her own: Edith Shreve at the Desert Laboratory, *Desert Plants* 8:23-29, 1986. [Interesting account of Shreve (1878-1956), whose career in plant physiology was sidetracked by motherhood and, typical for those times, womanhood. Shreve's husband was Forrest Shreve, author with I. L. Wiggins of *Vegetation and Flora of the Sonoran Desert*, 1964.]

CARTER, A., Aspectos generales de la flora de Baja California, *Cactaceas y suculentas Mexicanas* 31:79-96, 1986. [With 7-page English version. Since the submission of this article some years ago, various nomenclatural changes were made that have not been brought up to date in this paper; nor did the author have the opportunity of including in the bibliography I. L. Wiggins's *Flora of Baja California* (1980), which was published after the paper was written. In addition, because of the tremendous time lag for mail between Mexico and the United States, there was no opportunity to correct page proof—hence such inadvertencies as *Hystis* for *Hyptis* (p. 88) and *Dalia* for *Dalea* (p. 89).]

VEGETATION OF THE BALD HILLS OAK WOODLANDS, REDWOOD NATIONAL PARK, CALIFORNIA

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ABSTRACT

Composition and structure are determined for stands of bald hills *Quercus garryana* (Oregon white oak) woodland in Redwood National Park, California. Seven distinct plant community types are found. Distribution of the three most widespread types is related to moisture, slope position, and fire history: 1) *Quercus/Cynosurus* (xeric woodlands); 2) *Quercus/Dactylis* (mesic woodlands); and 3) *Quercus/Symphoricarpos* (dense, young mesic stands). Four types occupy specific habitats within the park: 4) *Ribes/Phacelia* (rock outcrops); 5) *Arrhenatherum/Sherardia* (glades); 6) *Quercus/Delphinium* (seasonally moist areas within xeric woodlands); and 7) *Philadelphus/Cystopteris* (stream channels).

Quercus garryana Dougl. (Oregon white oak) ranges from British Columbia to the Santa Cruz Mountains of California (Griffin and Critchfield 1972). Optimum development is reached in the Willamette Valley of Oregon, where *Q. garryana* dominates oak woodlands that occupy over 400,000 ha (Franklin and Dyrness 1973). In the North Coast Ranges of California, *Q. garryana* dominates the northern oak woodland and is a minor component of several forest types. The northern oak woodland consists of two distinct elements, a continuation of the interior foothill woodland and a coastal community type that is structurally distinct and known as "bald hills" oak woodlands (Griffin 1977).

Bald hills oak woodlands occur in the Coast Ranges of California from Humboldt and Trinity cos., southward to Napa Co. Approximately 19% of this area supports oak or oak-grassland vegetation (Wieslander and Jensen 1948, Storie and Wieslander 1952). Although the woodlands occur between 75–1600 m elevation throughout the region, they are best developed along ridgetops and upper south-facing slopes in Humboldt and Mendocino cos. The bald hills oak woodlands are structurally distinguished by a patchy mosaic pattern of dominance by either oak or grasses and not the balanced mixture of oaks and grassland found elsewhere in California (Clark 1937).

Thilenius (1968) describes the vegetation of Willamette Valley oak woodlands as seral and derived from open oak savannahs by

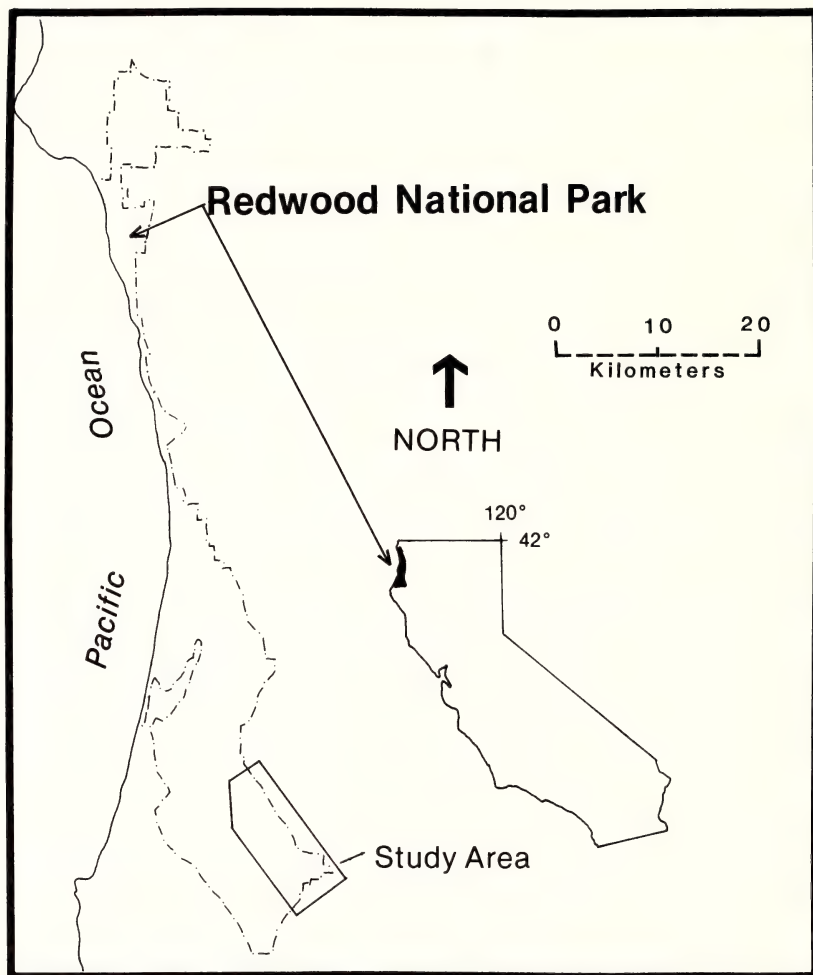


FIG. 1. Location of the study area within Redwood National Park and California.

the exclusion of fire. He defines four plant communities primarily by their shrub layers. Sugihara et al. (1983) found three stand structural types in the oak woodlands of Redwood National Park (RNP): 1) open savannah stands composed of all size classes and dominated by a few, large, widely scattered individuals; 2) closed-canopy stands of numerous, uniformly medium-sized, clustered trees; and 3) dense closed-canopy stands with uniformly small, single-stemmed individuals. Hektner et al. (1983) describe the vegetation composition and dynamics after disturbance of the open bald hills grassland outside the oak-grass mosaic. No other studies describe the flora or vegetation succession of the coastal bald hills. The purpose of this



FIG. 2. A view, looking northwest from Schoolhouse Peak, of the oak/grass mosaic and study area. Best development of the woodland is near the ridges, with redwood forests downslope.

study is to describe and classify the present vegetation in the northern range of the bald hills oak woodlands. Results of this study of present conditions will contribute to the potential for restoration and maintenance of the woodlands as a natural ecosystem. These baseline data will help assess the effects of the future management of the ecosystem.

STUDY AREA

Location. The 250 ha study area (Figs. 1, 2) is located within the Redwood Creek basin of RNP in Humboldt Co. and is representative of the northern extent of the bald hills oak woodlands. The area lies 8–22 km from the coast and 85–95 km south of the Oregon border. Redwood Creek flows from the southeast to the northwest and empties into the ocean at Orick, California. The grassland/woodland mosaic ranges in elevation from the banks of Redwood Creek (75 m) to near the top of Schoolhouse Peak (945 m) on the northeast slope above Redwood Creek.

Climate. Regional climate is Mediterranean, with strong oceanic influence at lower elevations in the northwest portion of the study area where summer fog frequently occurs. Approximately 90% of the total annual precipitation falls between October and May. Average annual rainfall ranges between 178 cm and 203 cm with snow

rarely falling except at higher elevations (Coghlan 1984). The mean daily maximum temperature in July is 25°C with absolute maxima rarely exceeding 38°C. The mean daily minimum in January is 2°C. Absolute minima rarely go below -7°C (Humboldt State Univ. 1974).

Geology and soils. Geologic substrate of the study area is residuum and colluvium from Franciscan siltstone, sandy siltstone, and gray-wacke sandstone. The landscape is characterized by numerous earthflows. A complex pattern of Inceptisol, Alfisol, and Ultisol soils underlies the woodlands, adjacent forests, and grasslands. Subsoil properties largely reflect geologic substratum and relief. Forest soils lack the umbric epipedon found in woodland and prairie soils, but all of these subsoils have a similar range of properties. Consistent soil patterns that correspond with forest/woodland/grassland boundaries have not been established (J. Popenoe pers. comm.).

Historical use. Native Americans regularly set fire to the bald hills for at least 6000 years prior to 1864, and these fires profoundly affected vegetation patterns (Thompson 1916, Lewis 1973, Bickel 1979, King and Bickel 1980, Benson 1983, Hayes 1985). Livestock grazing that was initiated by European settlers resulted in the establishment of many aggressive, non-native range plants, and was discontinued by the National Park Service in 1982. Extensive logging of adjacent redwood and Douglas-fir forests has been the primary disturbance factor affecting vegetation in the Redwood Creek basin from the 1940's until acquisition by the Park Service in 1978.

METHODS

Field reconnaissance of the study area revealed several plant assemblages within the oak woodland with distinct structure and composition. These assemblages were sampled by placing a total of 56 relevé plots averaging 750 m in homogeneous vegetation within uniform habitats (Mueller-Dombois and Ellenberg 1974). A list of all vascular plant species in each plot was compiled by height strata. Visual estimates of cover for the canopy, shrub, and herbaceous layers, as well as of each species, were made using the Braun-Blanquet (1932) cover scale: 1 = <1-5%, 2 = 5-25%, 3 = 25-50%, 4 = 50-75%, 5 = 75-100%. Aspect, slope, slope position, topographic configuration, oak stand type, exposure, and elevation of each plot also were recorded. Sampling was completed from May-July 1983, which coincides with the flowering and fruiting periods of most species. Nomenclature generally follows Munz (1973). Voucher specimens are on file at RNP.

Floristic characterization is based on species cover, percent occurrence, and fidelity. The stand classification is interpreted at a division level where the stand groups best represented the vegetation

TABLE 1. SYNOPTIC TABLE OF HIGH PRESENCE SPECIES IN OAK WOODLANDS BY VEGETATION TYPE. All species with less than 0.50 presence within the type are omitted. The first figure is the modal cover for each species found in the plots, based on Braun-Blanquet (1932). The second figure is the species presence for all plots within each vegetation type. Qu/Sy = *Quercus/Symphoricarpos*, Qu/Da = *Quercus/Dactylis*, Qu/De = *Quercus/Delphinium*, Ph/Cy = *Philadelphus/Cystopteris*, Ri/Ph = *Ribes/Phacelia*, Qu/Cy = *Quercus/Cynosurus*, Ar/Sh = *Arrhenatherum/Sherardia*. N = native species, I = introduced species.

Life form Species	Vegetation types (number of plots)						
	Qu/Sy (9)	Qu/Da (12)	Qu/De (12)	Ph/Cy (4)	Ri/Ph (4)	Qu/Cy (6)	Ar/Sh (9)
Trees							
<i>Pseudotsuga menziesii</i> (N)	1-0.89	1-0.75	1-0.58			1-0.50	
<i>Acer macrophyllum</i> (N)				1-1.00			
<i>Quercus garryana</i> (N)							
Seedlings	2-1.00	1-0.92	1-1.00	1-1.00	1-1.00	1-1.00	
Trees	5-1.00	5-1.00	5-1.00	4-1.00	3-1.00	5-1.00	
Shrubs							
<i>Symphoricarpos rivularis</i> (N)	2-1.00			1-1.00	1-0.75		
<i>Rhus diversiloba</i> (N)	1-1.00	1-0.92			2-1.00	1-0.67	
<i>Holodiscus discolor</i> (N)				2-1.00	2-0.75		
<i>Philadelphus lewisii</i> (N)				3-1.00	3-0.50		
<i>Ribes roezlii</i> (N)	1-0.56				2-1.00		
<i>Rosa pisocarpa</i> (N)				1-1.00	1-0.50		
<i>Amelanchier pallida</i> (N)				1-0.75			
<i>Osmanthera cerasiformis</i> (N)				1-1.00			
<i>Rubus vitifolius</i> (N)	1-0.89			2-0.50	1-0.50	1-0.50	
Grasses							
<i>Trisetum cernuum</i> (N)	1-0.89	1-0.58	1-0.58	1-0.50			
<i>Dactylis glomerata</i> (I)	1-0.89	2-1.00	1-0.75	1-0.50	1-0.50	1-0.83	
<i>Melica subulata</i> (N)	1-1.00	2-1.00	2-0.92	1-1.00		2-0.67	1-0.67

TABLE 1. CONTINUED.

Life form Species	Vegetation types (number of plots)						
	Qu/Sy (9)	Qu/Da (12)	Qu/De (12)	Ph/Cy (4)	Ri/Ph (4)	Qu/Cy (6)	Ar/Sh (9)
<i>Bromus carinatus</i> (N)	2-1.00	1-1.00	1-0.92	1-0.50	1-0.50	1-0.50	2-0.67
<i>Bromus sterilis</i> (I)			1-0.83		1-0.75	1-1.00	
<i>Elymus glaucus</i> (N)	1-1.00	1-1.00	2-1.00	1-1.00	2-0.75	2-1.00	1-1.00
<i>Avena barbata</i> (I)					1-1.00		
<i>Agrostis hallii</i> (N)	1-1.00	1-0.58	1-0.50	1-0.50		1-1.00	1-0.78
<i>Cynosurus echinatus</i> (I)	1-0.56	1-1.00	1-0.92	1-1.00	1-1.00	3-1.00	2-1.00
<i>Poa pratensis</i> (I)	1-0.56		1-0.75			2-1.00	1-0.89
<i>Holcus lanatus</i> (I)	1-0.89	1-0.50	1-0.58	1-0.75	1-0.75	2-1.00	2-1.00
<i>Arrhenatherum elatius</i> (I)		1-0.58	1-0.83	1-0.50	1-0.75	2-1.00	3-1.00
<i>Bromus rigidus</i> (I)					2-1.00	1-0.67	1-0.67
<i>Festuca viridula</i> (N)			1-0.67		1-0.75		2-0.89
<i>Aira caryophyllea</i> (I)					1-0.50		1-0.89
<i>Bromus mollis</i> (I)						1-0.50	1-1.00
Ferns							
<i>Polystichum munitum</i> (N)							
<i>Cystopteris fragilis</i> (N)	2-0.89		1-0.58	1-0.75	1-0.50		
<i>Cheilanthes gracillima</i> (N)				1-1.00			
<i>Polypodium glycyrrhiza</i> (N)							
<i>Pteridium aquilinum</i> (N)				1-0.75			3-0.56
Forbs							
<i>Galium nuttallii</i> (N)		1-0.92					
<i>Satureja douglasii</i> (N)	3-1.00	2-0.92					
<i>Polygala californica</i> (N)		1-0.50					

TABLE 1. CONTINUED.

Life form Species	Vegetation types (number of plots)						
	Qu/Sy (9)	Qu/Da (12)	Qu/De (12)	Ph/Cy (4)	Ri/Ph (4)	Qu/Cy (6)	Ar/Sh (9)
<i>Ligusticum apiifolium</i> (N)	1-1.00		1-0.50				
<i>Fragaria californica</i> (N)	2-1.00	1-1.00		1-0.50		1-0.50	
<i>Chlorogalum pomeridianum</i> (N)	1-0.78	1-0.83		1-0.50	1-0.75		
<i>Cynoglossum grande</i> (N)	1-0.89						
<i>Lathyrus vestitus</i> (N)	1-0.67	2-0.67	1-0.58	1-1.00	2-1.00		
<i>Phacelia heterophylla</i> (N)							
<i>Circaea alpina</i> (N)	1-0.56			1-1.00			
<i>Claytonia perfoliata</i> (N)	1-0.78		2-1.00	1-0.75	1-1.00		
<i>Trillium chloropetalum</i> (N)	1-1.00		1-0.50	1-1.00			
<i>Silene californica</i> (N)				1-0.50	1-1.00		
<i>Delphinium trollifolium</i> (N)			4-0.83	2-1.00	2-0.50		1-0.56
<i>Galium aparine</i> (I)	1-1.00	1-0.92	2-1.00	1-1.00	2-1.00	1-1.00	
<i>Osmorhiza chilensis</i> (N)	1-0.89	2-1.00	1-1.00	1-1.00	1-0.50	1-1.00	
<i>Sanicula crassicaulis</i> (N)	1-1.00	2-1.00	1-0.92	2-1.00	1-1.00	2-1.00	
<i>Brodiaea ida-maia</i> (N)	1-1.00	1-0.67	1-0.67	1-0.50	1-1.00	1-0.50	1-0.78
<i>Vicia americana</i> (N)	1-0.89	2-0.83	1-0.92	1-0.50	1-0.50	1-0.83	1-0.67
<i>Cerastium arvense</i> (N)	1-0.89						
<i>Caulalis microcarpa</i> (N)		1-0.92	1-0.58	1-1.00	2-1.00	1-0.67	1-0.89
<i>Marah oreganus</i> (N)	1-1.00		1-0.75	1-1.00	1-1.00	1-0.50	1-1.00
<i>Ranunculus occidentalis</i> (N)		1-0.83	1-0.92	1-0.75	1-0.50	1-0.83	1-0.89
<i>Taraxacum officinale</i> (I)			1-0.50	1-0.50		1-1.00	
<i>Hypochoeris radicata</i> (I)			1-0.50		1-1.00	1-1.00	1-0.67
<i>Cirsium vulgare</i> (I)		1-0.50				1-0.83	1-1.00
<i>Plantago lanceolata</i> (I)		1-0.75		1-0.50		1-1.00	1-1.00
<i>Rumex acetosella</i> (I)			1-0.75		1-1.00	3-1.00	2-1.00
<i>Sherardia arvensis</i> (I)							1-0.89

types observed in the field. One-hundred thirty-five species with frequencies greater than 5% were entered into TWINSpan, a computer analysis procedure in the Cornell Ecology Program (CEP) series (Hill 1979a). TWINSpan is a program for two-way indicator species analysis, a polythetic divisive method for community classification. The program was run with all default options except for the definition of pseudospecies cut-levels. Four cut-levels were defined as follows: level 1 = 1–5% cover, level 2 = 6–25% cover, level 3 = 26–50% cover, and level 4 = 51–100% cover.

The classified stands and 135 species are ordinated by detrended correspondence analysis using the DECORANA program in the CEP series (Hill 1979b) to reveal any additional dimension of the stand-group relationship. The DECORANA procedure was run with all default values and options. Comparisons of physiographic data with distribution of community types on the ordination graph and field observations produced environmental interpretations of plant community relationships. Plant community descriptions were then developed and used to classify and map the vegetation within the study area.

RESULTS

Three-hundred five species were found during sampling. Analysis by TWINSpan identified seven plant communities with three distinct structural forms: tree-dominated, shrub-dominated, and grass-dominated (Table 1). Four communities contain *Q. garryana* as the main structural unit. Two communities have shrubs composing the main structural unit with some *Q. garryana* present. The other community is dominated by grasses with mature *Q. garryana* absent. Within each life form category, species are ordered by relationships to one another. In general, species with mesic habitats are followed by those occurring in more xeric habitats. The distribution of the classified stands in floristic ordination space is shown in Fig. 3. Environmental features of the areas supporting the seven vegetation types are presented in Table 2.

Descriptions of the plant communities are based on Tables 1 and 2. Vegetation types are named for a combination of two species. The first is a dominant member of the main structural element. The second is a characteristic species with high cover and presence. The names reflect the mosaic pattern where oaks are either dominant or nearly absent. Important associates are species with high modal cover and presence.

Quercus/Symphoricarpos (Qu/Sy): This woodland type is found mid-slope in uniform, extremely dense stands of 25–40 yr-old, small-diametered oaks. *Symphoricarpos rivularis* forms most of the well developed low shrub layer. This type has the densest understory with the greatest number of shrub species and highest shrub cover

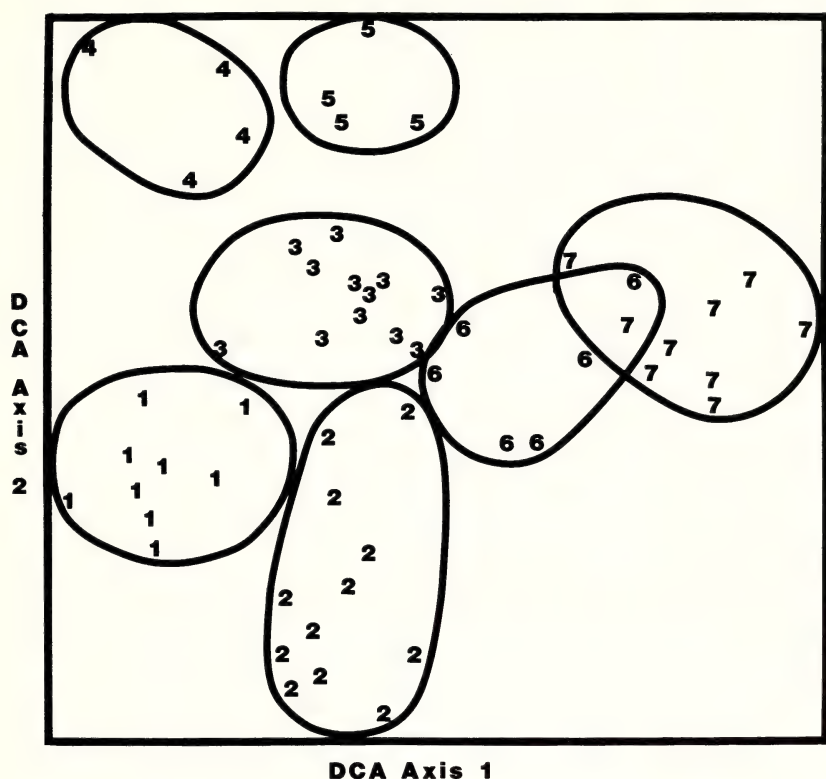


FIG. 3. Ordination graph showing the floristic relationships between plots. 1 = *Quercus/Symphoricarpos*, 2 = *Quercus/Dactylis*, 3 = *Quercus/Delphinium*, 4 = *Philadelphus/Cystopteris*, 5 = *Ribes/Phacelia*, 6 = *Quercus/Cynosurus*, 7 = *Arrhenatherum/Sherardia*.

(30%) of any oak-dominated type. Forbs dominate the herbaceous layer with only scattered grasses present. Important associates in the perennial forb-dominated herb layer include *Polystichum munitum*, *Satureja douglasii*, *Fragaria californica*, and *Bromus carinatus*. *Ligusticum apiifolium*, *Rubus vitifolius*, *Cynoglossum grande*, *Cerasium arvense*, and *Festuca occidentalis* are the more commonly encountered species that characterize this type.

Quercus/Dactylis (Qu/Da): This mesic woodland type is extensive on lower concave slopes associated with uniform, medium-sized oak stands. A mixture of tall, perennial grasses and perennial forbs dominates the understory. The shrub layer is very sparse. Important associates include *Dactylis glomerata*, *S. douglasii*, *Osmorhiza chilense*, *F. californica*, *Sanicula crassicaulis*, and *Vicia americana*. *Galium nuttallii*, *Lonicera hispidula*, and *Stachys rigida* are common characteristic species.

TABLE 2. GENERAL CHARACTERISTICS OF OAK WOODLAND VEGETATION TYPES. Acronyms are listed in Table 1. ¹ = Whittaker (1960); ² = Sugihara et al. (1983).

Characteristic	Vegetation types						
	Qu/Sy	Qu/Da	Qu/De	Ph/Cy	Ri/Ph	Qu/Cy	Ar/Sh
Mean plot elevation (m)	710	250	785	755	785	715	750
Mean slope (%)	30	35	35	35	30	25	35
Typical exposure	WNW	SW	W	W	WSW	S	NW
Mean Whittaker moisture index ¹	7	5	8	1	8	8	7
Typical slope position	mid	lower	upper	upper	upper	upper	mid
Typical topographic configuration	even	concave	concave	concave	convex	convex	concave/ convex
Typical stand type ²	dense	clustered	clustered	all	savannah	savannah	absent
Oak density (stems/ha) ²	4500– 12,000	740– 2500	740– 2500	variable	60–530	60–530	0
Mean canopy cover (%)	83	87	82	53	49	87	0
Mean shrub cover (%)	30	1	1	85	55	1	0
Mean herbaceous cover (%)	84	69	84	50	35	91	96
Mean number of species per plot	48	43	38	52	51	44	38
Native high presence species (% of total)	85	74	68	82	75	53	50

Quercus/Cynosurus (Qu/Cy): This xeric woodland type is dominated by shorter perennial and annual grasses with forb cover relatively low. The shrub layer is not well developed. This xeric type was the most heavily disturbed by grazing and occupies the upper, convex, south-facing slopes with oak stands containing a wide range of sizes and ages. Important associates include *Cynosurus echinatus*, *Holcus lanatus*, *Elymus glaucus*, *Poa pratensis*, *Arrhenatherum elatius*, *S. crassicaulis*. *Taraxacum officinale* is the most common characteristic species.

Quercus/Delphinium (Qu/De): Found on upper, concave slopes in uniform, medium-diametered oak stands, this type is restricted to concave topography on otherwise xeric slopes. In the spring and early summer, perennial forbs heavily dominate the understory of this distinctive woodland type. Forbs die back and grasses become dominant as the soil dries by mid-July, but the shrub layer remains sparse. *Delphinium trolliifolium* is the strong, early season dominant and *Dentaria californica*, *Lithophragma affine*, *Claytonia perfoliata*, and *Isopyrum stipitatum* are characteristic early season species. Important late season associates include *Galium aparine*, *Melica subulata*, and *E. glaucus*.

Arrhenatherum/Sherardia (Ar/Sh): Open glades dominated by perennial and annual grasses are found as narrow openings running up the slope within the oak stands. Shrubs are present only in scattered patches. These glades and the surrounding oaks form the distinctive oak/grass mosaic characteristic of the bald hills oak woodlands. Important associates include *A. elatius*, *H. lanatus*, *Festuca viridula*, *C. echinatus*, and *Rumex acetosella*. *Sherardia arvense*, *Lotus micranthus*, *Viola praemorsa*, *Aira caryophyllea*, and *Bromus mollis* are the common characteristic species. All of these species also are components of the open bald hills prairies. Many of the more abundant woodland species, however, such as *G. aparine*, *O. chilensis*, and *S. crassicaulis*, are absent from the Ar/Sh type.

Philadelphus/Cystopteris (Ph/Cy): This rocky stream channel type is composed of a dense shrub layer and a scattered herb layer of perennial forbs. The oak canopy is composed of a variety of stand types that range from very dense, small-diametered to large, broadly branched individuals. Canopy trees are found on the banks above the incised stream channels with their crowns extending over the channel but not rooted in the channel. *Philadelphus lewisii* and *Holodiscus discolor* dominate the tallest shrub layer found in these bald hills oak woodlands, and often reach a height of 7 m. *Sanicula crassicaulis* and *D. trolliifolium* are important associates in the herb layer. Characteristic shrubs include *Rosa pisocarpa*, *Amelanchier pallida*, and *Osmaronia cerasiformis*. *Cystopteris fragilis*, *Polypodium glycyrrhiza*, and *Tellima grande* are characteristic members of the herb layer.

Ribes/Phacelia (Ri/Ph): This rock outcrop type is composed of a moderately dense shrub layer and a scattered herb layer of perennial and annual forbs and grasses. The oak canopy is generally present although often not well developed. When trees are present they usually grow adjacent to the outcrops and frequently shade them. *Ribes roezlii* and *Rhus diversiloba* dominate the shrub layer. Important associates in the herb layer include *G. aparine*, *Caucalis microcarpa*, and *Bromus rigidus*, *Phacelia heterophylla*, *Silene californica*, *Cheilanthes gracillima*, and *Avena barbata* are the common characteristic species. Notably uncommon on the rock outcrops are the grasses such as *H. lanatus*, *Agrostis hallii*, *M. subulata*, and *Trisetum cernuum*, which are abundant in the understory of the open woodlands.

DISCUSSION

The indirect ordination (Fig. 3) resulted in clustering of plots in two dimensional space corresponding to the seven plant community types. The left end of DCA axis-one represents dense stands in mesic locations with less historic grazing disturbance and a lower representation by introduced species. The Ar/Sh type occurs at the far right. These open glades without summer shade sustained the greatest grazing impact. The lower half of DCA axis-2 represents well developed continuous soils. Rock outcrops and rocky stream channels occur at the top of the ordination. The Qu/De occurs on rocky soils and appears intermediate between the types characteristic of outcrops and well developed soils.

Oak/grassland mosaic. The distinctive oak/grassland mosaic characteristic of the bald hills oak woodlands is best developed in the southeast corner of RNP. This pattern occurs primarily on higher ridges, but is continuous downslope on earthflows with southern exposures. Mid-slope oak woodlands are extensive and associated with occasional glades and a large central open prairie. At low elevations and closer to the coast, the prairie becomes the primary feature, with *Q. garryana* stands restricted to forest margins and narrow projections into the grasslands. Oak woodlands extend downslope to Redwood Creek at elevations of less than 100 m in several locations. In mesic low elevation and coastal areas within the fog zone, *P. menziesii* forest has colonized former oak woodlands during the past 130 years. Low elevation stream channels and rock outcrops are converted completely to this conifer forest, and only the open woodlands are left intact. The remaining outcrops and streamside vegetation occur only at mid- to upper elevations in the study area. The remaining open woodlands are the Qu/Da type that is correlated with the mesic nature of the concave lower slopes within the fog belt.

Open woodlands. The Qu/Da, Qu/Sy, and Qu/Cy types comprise most of the area within the well developed open woodlands. Distribution of these three types is related to topography, slope position, grazing, and fire history. Qu/Da and Qu/Sy are found exclusively under closed-canopy oak stands on lower slopes and mid- to upper north-facing slopes. Aspect, sheltered topography, and frequent summer fog make these relatively mesic sites. The Qu/Da type is predominant on the lower slopes under stands of 70–100 yr-old oaks. Qu/Sy occurs under very dense stands of small-diameter oaks on upper north-facing slopes. These stands originated following a fire in 1948 (Sugihara et al. 1983). The two mesic woodland types are closely related floristically. Qu/Sy is probably a fire sere of Qu/Da. Qu/Sy is clearly distinguished from Qu/Da by the dense *S. rivularis*-dominated shrub layer characteristic of the Qu/Sy type. The third major woodland type, Qu/Cy, is found in oak stands composed of all size classes but dominated by widely-spaced, large-diameter trees. This association is found on upper, convex, south-facing slopes and along the ridgeline where moisture conditions are more xeric and grazing was the most intense.

Specialized habitats. The remaining four plant community types are confined to specialized habitats within the study area. Ar/Sh occurs in glades among the oak stands and includes many species characteristic of the continuous open grassland adjacent to the study area. These include weedy introduced grasses and forbs such as *A. elatius*, *C. echinatus*, *A. caryophyllea*, *Trifolium dubium*, *Trifolium subterraneum*, *Linum bienne*, *H. lanatus*, *R. acetosella*, *Plantago lanceolata*, *Hypochoeris radicata*, and *Pteridium aquilinum* (Hektner et al. 1983). Glades also are related floristically to the xeric Qu/Cy woodland, but not limited to xeric topographic positions within the study area. Qu/De is found on relatively moist concave slopes within xeric Qu/Cy woodlands. Dominance of native forbs, especially *D. troliifolium*, is especially evident in the early summer when the adjacent Qu/Cy type is dominated by immature grasses. Lack of canopy cover results in dominance by characteristic xeric woodland species in mesic physiognomic positions. Two minor community types are found in areas that have very little soil. The Ph/Cy type occupies incised, boulder-strewn stream channels on upper slopes. The numerous dry, exposed, rock outcrops are occupied by the Ri/Ph type. Both Ph/Cy and Ri/Ph are dominated by tall shrubs that thrive on the bare soil and rock surfaces not covered by a thick herbaceous mat.

Introduced species. Success of introduced species in the seven community types appears to be influenced by past grazing and fire. The most heavily grazed communities are grass-dominated and composed of the highest percentage of introduced species. Only 50%

of the high presence species found in Ar/Sh and 53% in Qu/Cy are native. Qu/De is dominated by native forb species with 68% of the high presence species native. Grazing impact on Qu/De was reduced by the lack of early summer grazing, which was restricted due to the toxicity to cattle of the early season dominant *Delphinium trolifolium*. Mesic woodlands supporting the Qu/Da type had 74% native species. Stream channels and rock outcrops were more protected from grazing because of inaccessibility. This is reflected in the 75% native species for Ri/Ph and 82% for Ph/Cy. The highest representation of native species in any vegetation type was the 85% found in the Qu/Sy community that was recently influenced by fire.

Relationship to other woodlands. Ecologically and floristically, these *Q. garryana* woodlands are more similar to those of the Willamette Valley of interior Oregon than to any other California woodland type. The bald hills oak woodlands, however, are distinct from the interior Oregon woodlands in structure, composition, and their coastal habitat (Thilenius 1968). Shrubs dominate all Willamette Valley plant communities, but in bald hills woodlands only the Qu/Sy type, stream channels, and rock outcrops support well developed shrub layers. In the Willamette Valley and the bald hills, stand structure was determined largely in the past by burning. Savannas with grassy openings between the individual trees that are characteristic of the Willamette Valley were not typical of woodlands in this area. Historical accounts indicate that *Q. garryana* was well-spaced in the pre-settlement stands of the bald hills, but the canopy was closed and alternated with the grasslands.

Fire and succession. Reduction of fire frequency during post-settlement times has altered succession in both the Willamette Valley and the bald hills. Succession is from oak savannah to oak forest, and then to *Pseudotsuga menziesii* forest in Oregon. In the bald hills, succession is from oak forest to mixed evergreen forest in the xeric interior areas, and to *Sequoia sempervirens*/*P. menziesii* at low elevation and coastal mesic areas (Sawyer et al. 1977). With the cessation of burning by Native Americans and introduction of wildfire suppression, succession to *P. menziesii* has progressed without natural control. Subsequent succession to *S. sempervirens* is seen in older mesic stands of *P. menziesii*. The absence of redwood forest on potential redwood sites supports archaeological evidence of constantly high fire frequency over several thousand years prior to European settlement.

Although allied more closely to the Willamette Valley woodlands than any California oak type, the bald hills oak woodlands are a unique feature of California's redwood region. The National Park Service has allowed the vegetation of bald hills to develop ungrazed for the first time in over a century. This study provides a description

of existing vegetation patterns in the northern bald hills. This baseline information is essential for the monitoring of vegetational changes occurring in response to management of oak woodlands in Redwood National Park.

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Members of the California Botanical Society have a long-term and apparently increasing interest in the botany of Mexico and Central and South America. Because of this interest, the editors believe our new policy will provide broader communication among scientists, will open the journal to a wider readership, and perhaps will increase membership in the CBS. We also hope it will extend a gesture of goodwill to our Hispanic colleagues and neighbors. We look forward to a successful bilingual journal and trust the membership will support this new policy.

UNA NUEVA POLITICA DE MADROÑO

A partir de esta fecha Madroño aceptará manuscritos redactados en Español. El primer artículo que se publicará dentro de esta nueva política aparecerá en el volumen 35(1); en cada volumen se publicarán un número limitado de artículos escritos en Español. Los autores deberán utilizar las convenciones editoriales de Madroño e incluir un resumen del trabajo en Inglés.

Los miembros de la Sociedad Botánica de California tienen un interés a largo plazo en la botánica de México, Centro y Sudamérica; dicho interés aparentemente se está incrementando. Por esta razón, los editores creemos que esta nueva política ampliará la comunicación entre los científicos, la revista estará al alcance de un mayor número de lectores y probablemente se extenderá un gesto de buena voluntad para con nuestros colegas y vecinos hispanoparlantes. Confiamos en el éxito de esta revista bilingüe y en el apoyo hacia esta nueva política por parte de los socios.

A FLORA OF VINA PLAINS PRESERVE, TEHAMA COUNTY, CALIFORNIA

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ABSTRACT

The 626 hectare Vina Plains Preserve is located in southernmost Tehama Co., California, and is a remnant of various native grassland habitats. Geologically, this region is a weathered fanglomerate formed from alluvial deposits of the Tuscan formation and later deposits of silt. A botanical survey of the Preserve between January 1982 and May 1987 resulted in the identification of 53 vascular plant families that included 287 taxa. Native species comprised 67% of the taxa, and annuals comprised 77%. Eight rare plant species were found, their distributions noted, and numbers estimated. All the plants occur in one or more of the six habitats, which include vernal pools, hogwallows, seeps, vernal marshes, uplands, and outcrops. Families with the most species include Poaceae (50), Asteraceae (36), Fabaceae (17), Boraginaceae (13), and Amaryllidaceae (10).

The original species composition of the pristine Californian grasslands is largely unknown (Bartolome and Gemmill 1981). The first direct evidence for the replacement of native perennial bunchgrass by introduced annual species on Californian grassland has been produced by a recent study of opal phytoliths at Jepson Prairie Reserve in Solano Co. (Bartolome et al. 1986). There is little detailed information on the composition of other similar Californian grasslands (Jokerst 1983). Published studies are available for the following areas of the northern Sacramento Valley: Richvale Vernal Pool Site, Butte Co. (Schlising and Sanders 1983), Jepson Prairie Nature Conservancy Preserve, Solano Co. (Holland 1981), Maidu Park, Placer Co. (Holland 1982), and Table Mountain, Butte Co. (Jokerst 1983).

The vernal pools of Californian grasslands contain a high proportion of endemic plants (Holland 1976). With increasing urbanization and the expansion of agribusiness, these habitats are disappearing except where they are protected by specific organizations. One such area of grassland and vernal pools is Vina Plains Preserve in Tehama Co., which is owned and managed by The Nature Conservancy. The purposes of this study were to conduct an inventory of all vascular plant species and their habitats on the Preserve, and to provide detailed information on the occurrence of rare plants.

STUDY AREA

Location. The Vina Plains Preserve is located in southernmost Tehama Co., in the northern portion of the great Central Valley of

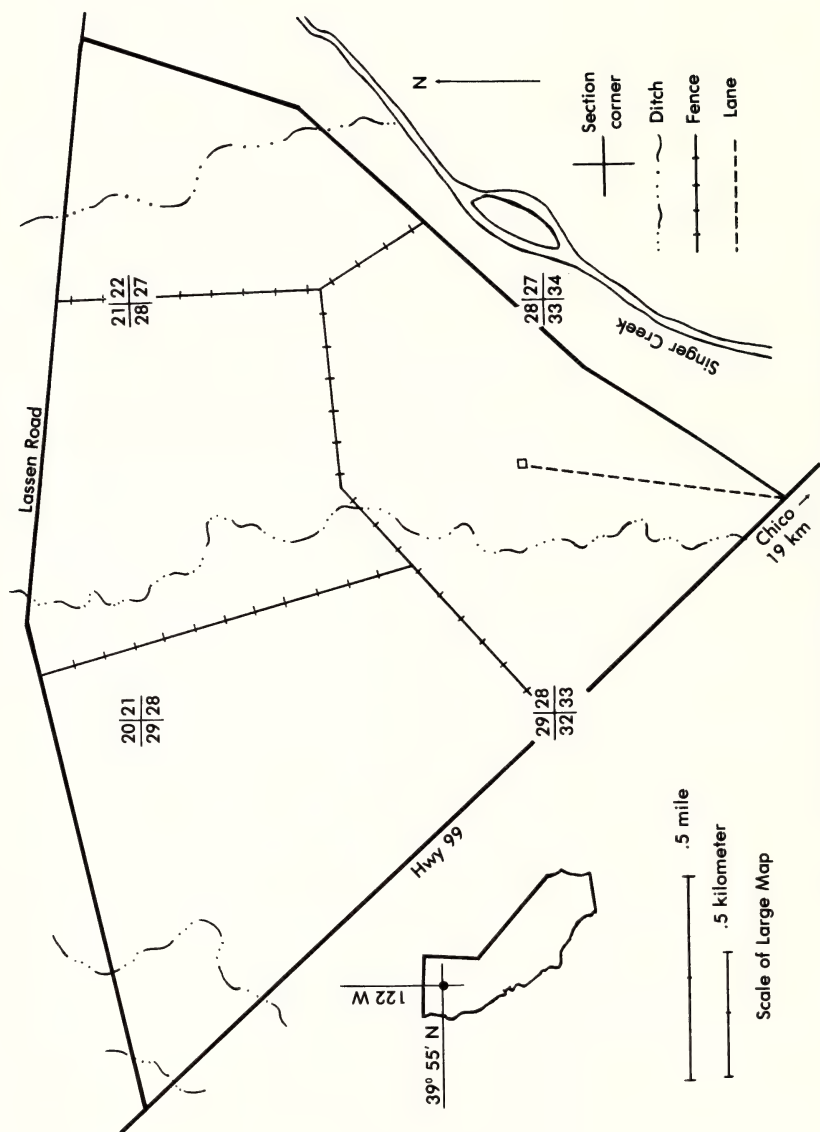


FIG. 1. Location of Vina Plains Preserve, Tehama County, California.

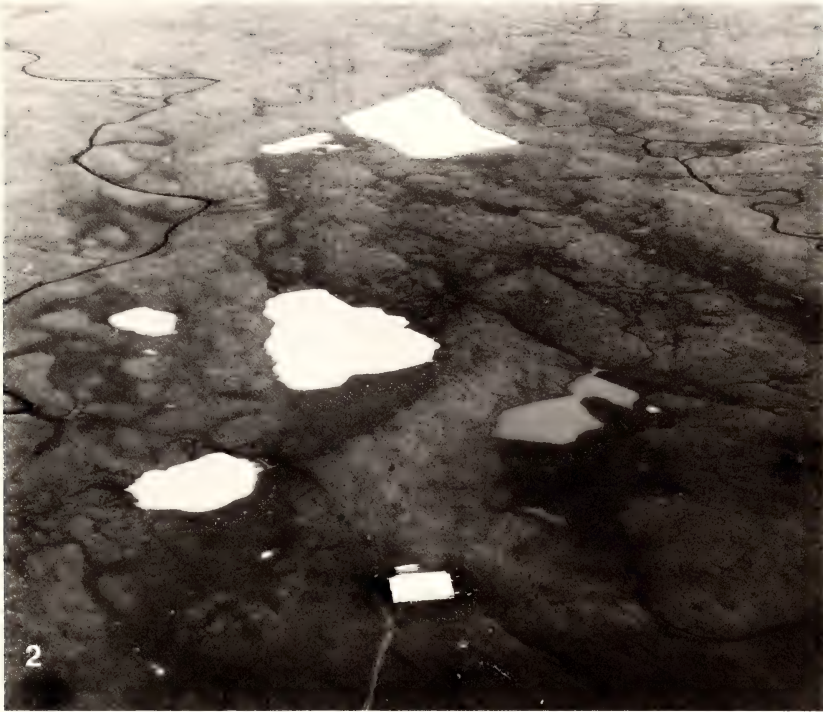


FIG. 2. Aerial view of the Vina Plains Preserve from the south, showing several large vernal pools and a barn located on the access road.

California (Fig. 1). The area is bordered by Tuscan volcanic mudflows of the Cascade Range to the east and the Sacramento River to the west. The elevation is about 66 m, and topographic relief varies by about 4.5 m from north to south. The Wurlitzer addition in 1984 (176 ha) is not included in the present study.

The study area is composed of flat or mounded, rolling grassland, interspersed by several kinds of wet areas (Fig. 2). These wet areas consist of: 1) four drainages that were deepened for irrigation in the past, and that traverse the parcel in a roughly north/south direction; 2) a number of vernal pools of varying sizes; and 3) many hogwallows (Fig. 3), smaller depressions, and natural drainages that hold water for short periods of time.

Geology and soils. The following theory of the formation of parent materials for the soils is based on information from J. W. Guyton (pers. comm.), a geologist at California State University, Chico. The oldest rock type in the area is an alluvial fan deposit. It was derived from the Tuscan formation composed of old volcanic mudflows that make up a considerable portion of the foothills from Red Bluff



FIG. 3. A large hogwallow that displays "rings" of flowering species. Mt. Lassen is visible in background.

southward to the Vina area (Harwood et al. 1981). This deposit consists of coarse sands and gravels that were transported from the foothills on the northeast and east, deposited in alluvial fans, and cemented. This "fanglomerate" is 1 to 2 million yr old, mainly andesitic and basaltic in composition, and well cemented into rock (conglomerate) by materials in the ground water. At Vina Plains Preserve, the strata are exposed in such places as the waterways and edges of the pools. About 100,000 yr ago, weathering weakened the cement, converting the conglomerate back to sand, silt, and gravel to a variable depth of 2–5 m. Subsequently (10,000–20,000 yr ago) the deposition of silt occurred either by wind or by flooding of the Sacramento River during the period of glacial climate. The fine-grained sediment is evident in isolated mounds. Finally, strong winds associated with a dry climate during the period that ended about 4000 yr ago (known as the altithermal) could have removed much of the silt layer and excavated pools in the weathered fanglomerate. The pools hold water because of the basic, slightly permeable fanglomerate floor, and because of the clay that washed in from the higher surroundings. Milder erosion by gentle runoff could have produced the many gullies that occur naturally.

The existing soils are largely of andesitic and basaltic composition, and are described as the "Tuscan series" (U.S.D.A. 1967). The surface is dark brown and cobbly; the subsoil is more reddish, clayey,

and gravelly, and is often exposed at the margins of pools and other eroded areas. Other series include the Keefers, similar to Tuscan, and Anita and Berrendos, that are more clayey. The deeper (Anita and Berrendos) soils are found commonly where pools have formed or in the drainage channels. All soils and pools have an underlying hardpan.

HABITATS AND VEGETATION

General trends during one field season indicated that the plants on the Preserve tend to group themselves into six general habitats, with some overlap or transition between habitats. For purposes of this study, these were termed upland, pool, hogwallow, seep, vernal marsh, and outcrop.

Upland. The majority of the terrain, consisting of rather well drained areas, is considered upland. The soil is mainly Tuscan loam: it is slightly acidic, with depth from a few centimeters to about one meter (U.S.D.A. 1967), and is slightly cobbly. Water runs off quickly and collects in the internal drainages. Species found in uplands are mainly annual grasses and forbs, such as *Lasthenia californica*, *Layia fremontii*, *Orthocarpus erianthus*, *Lepidium nitidum*, *Hemizonia fitchii*, several species of *Erodium*, *Navarretia*, *Vulpia*, and *Bromus*, and such perennials as *Dodecatheon clevelandii* subsp. *patulum* and *Brodiaea californica*.

Seeps. Areas that have at least some moisture supplied by slow-moving water during most of the year are considered seeps. These include margins of irrigation ditches and adjoining low areas. The soil is often deep and contains much silt. Such habitats are found along (east to west) Singer Creek Ditch, Sheep Camp Ditch, and two other ditches traversing the west pasture (Fig. 1). Typical species are: *Callitriche heterophylla* subsp. *bolanderi*, *Centaurium floribundum*, *Elatine heterandra*, *Limosella acaulis*, *Lythrum hyssopifolia*, *Mimulus guttatus*, *Crassula saginoides*, and *Ranunculus muricatus*. In some places, the plants occur in zones. For example, at one site *Eleocharis macrostachya* occurs in standing water of a ditch, *Ammannia coccinea* and *Diplachne fascicularis* on the muddy shore, *Echinochloa crusgalli* on adjacent damp grounds, and *Eragrostis cilianensis* with the last two.

Hogwallows. The hundreds of potholes, depressions, and internal drainages that have ephemeral standing water are considered hogwallows. The soil is usually thinner than in seeps. Hogwallows may have rocky bottoms and varying amounts of sand and silt. When silt is present, species occur that also are found in pools. Typical species of hogwallows are: *Lasthenia fremontii*, *Limnanthes douglasii* var. *rosea*, *Plagiobothrys stipitatus* var. *micranthus*, and *Down-*

ingia ornatissima or *D. bicolor*. Under optimum conditions, hogwallows display concentric colored "rings" of flowering species.

Pools. A "pool" is deeper and larger than a hogwallow and is presumed to have been formed by the blow-out process. The bottom is composed of clay or silt underlain by impermeable fanglomerate. Water accumulated during winter rains remains into late spring or early summer. The maximum depth of the different pools varies from 0.3–1.0 m; however, depth also fluctuates with seasonal rainfall and with drydown. Ten large pools were found to contain *Orcuttia pilosa* and *O. tenuis*.

The largest of these (located in the northern portion of the west pasture) measures about 345×142 m. The smallest (located in the northeast portion of the south pasture) measures 80×65 m. Most are in areas of Anita clay loam, but three are on Tuscan loam. All have some degree of silt or clay accumulated by erosion from surrounding higher ground. The deepest pool retained water (in 1982) into June, but most had no standing water by early to mid-May. In some, the margins are sandy, whereas in others there are many cobbles with heavy varnish that indicates great age. Typical species are: *Asclepias fascicularis*, *Eryngium vaseyi* var. *vallicola*, *Marsilea vestita*, *Navarretia leucocephala*, *Psilocarphus brevissimus*, *Downingia bella*, *D. bicornuta*, *Orcuttia pilosa*, *O. tenuis*, *Tuctoria greenii*, and *Chamaesyce hooveri*. Although there is a greater species richness on the upland, the species listed for pools (except *C. hooveri* and *Orcuttia tenuis*) usually occur in all the large pools.

Vernal marshes. The vernal marsh differs from the hogwallow habitat in its greater area and from the pool habitat in that it lacks deep, standing water. Water remains in the marsh habitat longer than in the hogwallows, but not as long as in the pools. The soil is thin Tuscan loam and often contains additional clay deposited from erosion. Species found here include primarily native annual forbs found in the pools and hogwallows, and some native annual grasses, which include those that are generally found in upland habitats and hogwallows. *Boisduvalia cleistogama* and *B. glabella*, native forbs found in the pools, are present in this habitat. Other typical species include: *Alopecurus saccatus*, *Limnanthes douglasii* var. *rosea*, and *Plagiobothrys stipitatus* var. *micranthus*.

Outcrops. This is a habitat of thin, poor, rocky or sometimes gravelly soil. These outcrops usually occur on the upland, but also occasionally are found within the dried pools. Usually, the outcrop is the driest habitat, and the plants are small, native or introduced annuals. Typical outcrop species are: *Crassula connata*, *Parvisedum pumilum*, *Koeleria phleoides*, and occasionally *Plantago erecta* and *P. bigelovii*.

FLORA

Summary. Fifty-three vascular plant families were found that consist of 287 taxa. Two other species (*Populus fremontii* and *Salix* sp.) have been extirpated by the razing of a man-made reservoir. Of the total taxa, 192 (67%) are native and 95 (33%) are introduced; 221 (77%) are annuals and 66 (23%) are perennials.

Rare plants. Eight species at Vina Plains Preserve are mentioned in the California Native Plant Society (CNPS) *Inventory of Rare and Endangered Plants of California* (Smith and York 1984). A ninth, *Paronychia ahartii*, is too recently described for listing, but is being considered for inclusion.

Astragalus pauperculus has been found scattered at a few sites on thin Tuscan soil where gaps in the vegetation occur. It is inconspicuous, and may occur more often than indicated. Smith and York (1984) list it as rare but not endangered, and endemic to California. Its Federal status is "widespread, not threatened."

Cuscuta howelliana was found in three of the pools and a hogwallow. Due to the twining, meandering nature of the plant, counts must be based on the number of host plants; these vary from a few (3–15) to many, covering about one fourth of one pool. Although not endangered (CNPS, Federal), this species is rare and endemic to California, and requires monitoring.

Chamaesyce hooveri was found in six of the pools and a hogwallow. Population size varied from a single plant in the hogwallow to about 3000 in the largest pool. Mature plants form mats up to one meter in diameter by late summer. It is rare and endemic to California and is endangered throughout its range (CNPS) because of loss of vernal-pool habitat. Insufficient data, however, are available for Federal listing.

Fritillaria pluriflora has been found at seven sites; all but one of these occurred in deep clay soil. Population size was from 15–30, and usually approached the latter. Although rare and endemic to California, it is considered endangered (CNPS) in only a portion of its range and is not on the Federal list.

Lepidium latipes has been found in a few hogwallows. A census in 1985 at one large hogwallow revealed a population of 584 plants. This species is rare, but not endangered in California, and is not on the Federal list.

Orcuttia pilosa was found in six pools, but occurred in large numbers in only the four deepest ones. Numbers were estimated in the thousands. It was found in association with *Tuctoria greenei* in only one pool. It is rare and endangered in California throughout its range (CNPS) due to reduction of habitat. Data are on file to support a Federal listing.

Orcuttia tenuis occurs in one small pool at the northeast corner of the Preserve. Numbers were estimated at 5000–10,000 plants. A second germination took place following mid-summer rains in 1982, and this population was estimated at about 1000 plants. The status of this species is similar to *O. pilosa*.

Paronychia ahartii Ertter was found at one location in the eastern portion of the Preserve in April 1984. It was known previously only from a few, widely separated areas in northern California, from collections made by J. T. Howell, and from the Lowell Ahart Ranch in Butte Co. (J. Jokerst pers. comm.). It is being considered for CNPS listing; more data are needed to support a Federal listing.

Tuctoria greenei is more widespread than *Orcuttia pilosa* or *O. tenuis*. Most populations of it are smaller and usually consist of a few hundred plants; however, about 30,000 plants have occurred in one exceptional pool. Tufting makes accurate counts difficult to obtain. This is a rare endemic of California and is endangered throughout its range due to reduction of habitat (CNPS). Data are on file to support a Federal listing.

Annotated catalogue. The following list includes all species collected between late January–October 1982 and March–May 1983. Seven additions have been made from 1984–1987. Fifty-two visits were made in the original study, most frequently during the peak flowering season. Voucher specimens are housed at CHSC. Nomenclature follows Munz (1959, 1968). Current regional authorities are followed whenever possible. Synonyms are included if names differ from Munz. Each entry includes information on habitat and flowering phenology at the Preserve, and whether the species is annual (A), biennial (B), perennial (P). If the plant is not native to the area, it is marked with an asterisk. Occurrence of most species is noted as abundant, common, occasional, and uncommon. Rare plants listed in Smith and York (1984) are noted.

VASCULAR PLANTS OF VINA PLAINS PRESERVE

LEPIDOPHYTA

Isoetaceae

Isoetes howellii Engelm. P; standing water of seeps, hogwallows, and pool margins.
Isoetes nuttallii A. A. Eat. P; habitat as for *I. howellii*, but appears earlier in spring.

PTEROPHYTA

Marsileaceae

Marsilea vestita Hook. & Grev. P; abundant in vernal pools, occasional in hogwallows.
Pilularia americana A. Br. P; standing water of irrigation ditches, occasional at margins of pools.

ANTHOPHYTA—DICOTYLEDONEAE

Amaranthaceae

- **Amaranthus albus* L. A, common; dried pools and low places; Jul–Sep.
Amaranthus blitoides Wats. A; disturbed areas; Jun–Aug.

Apiaceae

- **Anthriscus scandicina* (Weber) Mansf. A, occasional; upland; Feb.
Eryngium vaseyi Coult. & Rose var. *vallicola* (Jeps.) Munz. B or P, locally abundant; vernal wet areas; Jun–Jul.
Lomatium humile (Coult. & Rose) Hoov. ex Math. & Const. P, common; upland, on gentle slope or depression; Tuscan loam; Mar–Apr.
Sanicula bipinnatifida Dougl. ex Hook. B or P, common; upland slope or shallow depression; Tuscan loam or deeper soils; Mar–Apr.

Asclepiadaceae

- Asclepias eriocarpa* Benth. P, occasional; upland; Jun.
Asclepias fascicularis Dene. in A. DC. P; abundant in dried pools, occasional long internal drainages and ditches; Anita clay or Tuscan or Keefers loam; Jun–Sep.

Asteraceae

- Achyrachaena mollis* Schauer. A; hogwallows and upland where heavier soils hold moisture; Apr.
Blennosperma nanum (Hook.) Blake. A, common; hogwallows and vernal marshes, shallow to deep; thin or cobbled soils or clay; Feb–Mar.
 **Centaurea solstitialis* L. A, widespread, especially on disturbed soil; May–Aug.
 **Conyza canadensis* (L.) Cronq. A; scattered locations of upland; Tuscan and Keefers loam; Aug–Sep.
Evax acaulis (Kell.) Greene. A, occasional; upland or hogwallow; May–Apr.
Evax caulescens (Benth.) Gray. A; vernal moist areas, especially pool edges and hogwallows; clay soil; Apr–Jun.
 **Filago gallica* L. A, occasional; disturbed Tuscan loam; Apr–May.
 **Gnaphalium luteo-album* L. A, common, especially on disturbed sites; Jul.
Hemizonia fitchii Gray. A, common; entire Preserve except wet areas; May–Sep.
Hemizonia luzulaefolia DC. subsp. *rudis* (Benth.) Keck. A; hogwallow areas and, to a lesser extent, borders of seeps; more gregarious than *H. fitchii* but less widespread; Jul–Sep.
 **Hypochoeris glabra* L. A, common; upland, vernal marsh, and hogwallow; May–Jun.
 **Lactuca saligna* L. A; scattered locations of upland, especially in disturbed areas; Jul–Aug.
 **Lactuca serriola* L. A; more common than the previous species but similar habitat; Aug.
Lagophylla glandulosa Gray subsp. *glandulosa*. A, abundant; upland on thin or clayey Tuscan loam; Jun–Sep.
Lagophylla glandulosa Gray subsp. *serrata* (Greene) Keck. A, common; upland open slopes; thin Tuscan loam; May–Jun.
Lasthenia californica DC. ex Lindl. [*L. chrysostoma* (Fisch. & Mey.) Greene] A, common; widespread in many habitats except wettest or most drained; Mar–May.
Lasthenia fremontii (Torr. ex Gray) Greene. A, common; widespread in hogwallows and margins of pools, less so on drained upland; Tuscan loam or sometimes deeper soils; Mar–May.
Lasthenia glaberrima DC. A; dried pools; May–Jun.
Lasthenia glabrata Lindl. subsp. *coulteri* (Gray). A; upland; Apr.

- Lasthenia platycarpa* (Gray) Greene. A, locally common; hogwallows or wet upland; Feb–Apr.
- Layia fremontii* (T. & G.) Gray. A; ubiquitous on upland and bordering hogwallows; Feb–May.
- **Leontodon leysseri* (Wallr.) G. Beck. A, common; Tuscan or deeper soil of upland, or near seeps; Jun.
- **Leontodon taraxacoides* (Vill.) Meart. A; Tuscan loam or heavier soils of upland, or near seeps; May.
- Lessingia nana* Gray in Benth. A, abundant; upland; Jul–Aug.
- Matricaria matricarioides* (Less.) Porter. A, common on disturbed sites; Mar–Jul.
- Micropus californica* F. & M. A, common; dried hogwallows or open upland; Tuscan loam; Apr–May.
- Microseris acuminata* Greene. A; upland; Apr.
- Microseris douglasii* (DC.) Sch.-Bip. subsp. *douglasii*. A; upland or hogwallows; Tuscan loam; Apr.
- Microseris douglasii* (DC.) Sch.-Bip. subsp. *tenella* (Gray) Chamb. A, occasional; upland; Tuscan loam or deeper soils; May.
- Psilocarphus brevissimus* Nutt. A, common; dried vernal pools, hogwallows, and vernal marshes; Apr–Jun.
- Psilocarphus oregonus* Nutt. A, less common than the preceding species; habitat and phenology similar.
- **Senecio vulgaris* L. A; disturbed areas; Jan–Sep.
- **Silybum marianum* (L.) Gaertn. A, occasional; near irrigation ditches; May.
- **Sonchus asper* L. A, occasional; Jul.
- **Sonchus oleraceus* L. Similar to *S. asper*.
- **Xanthium strumarium* L. var. *canadense* (Mill.) T. & G. A; dried vernal pools, abundant in some; Jul–Aug.

Boraginaceae

- Amsinckia intermedia* F. & M. A; found on a grassy slope near a fence; Apr.
- Amsinckia menziesii* (Lehm.) Nels. & Macbr. A; found with *A. intermedia*; Apr.
- **Heleotropium europaeum* L. A; scattered locations on upland; Tuscan or clay loam; Aug–Sep.
- Plagiobothrys austinae* (Greene) Jtn. A; vernal wet, slight depressions; Tuscan or deeper soils; Mar–Apr.
- Plagiobothrys canescens* Benth. A; occasional populations on upland; May–Jun.
- Plagiobothrys fulvus* (H. & A.) Jtn. var. *campestris* (Greene) Jtn. A; occasional populations on upland; Mar–Apr.
- Plagiobothrys glyptocarpus* (Piper) Jtn. A; seeps; Tuscan or Keefers loam; Apr–May.
- Plagiobothrys greenei* (Gray) Jtn. A; hogwallows and other slight, vernal wet depressions; Tuscan or deeper soils; Mar–Apr.
- Plagiobothrys humistratus* (Greene) Jtn. A; phenology and habitat as for *P. scriptus*. According to Schlising (1984), may be conspecific.
- Plagiobothrys leptocladus* (Greene) Jtn. A; seeps and shallow hogwallows; Tuscan or heavier soils; Apr–May.
- Plagiobothrys scriptus* (Greene) Jtn. A, uncommon; upland on thin Tuscan or deeper soils, sometimes hogwallows; prostrate and inconspicuous; Feb–Mar.
- Plagiobothrys stipitatus* (Greene) Jtn. var. *micranthus* (Piper) Jtn. A; pools (mostly) and hogwallows; Mar–Jun.
- Plagiobothrys stipitatus* (Greene) Jtn. var. *stipitatus*. A; hogwallows; Mar–Apr.

Brassicaceae

- Athyas pusillus* (Hook.) Nutt. A; occasional populations in many habitats except wettest; Feb–Mar.
- **Brassica campestris* L. A; occasional on disturbed soil; Apr–May.

- **Capsella bursa-pastoris* (L.) Medic. A, common; disturbed areas; Feb–Apr.
Cardamine oligosperma Nutt. A, occasional; Tuscan loam or deeper soils; Mar–Apr.
Draba verna L. A, scattered locations on vernal moist upland; thin soil; Mar–Apr.
Lepidium lasiocarpum Nutt. A, occasional; clayey soil; Apr.
Lepidium latipes Hook. A; found at two sites: several small, scattered populations in hogwallows near barn in south pasture; single, larger population in deep soil near irrigation ditch in south pasture; Mar.
Lepidium nitidum Nutt. A, common and widespread; Feb–Mar.
 **Raphanus raphanistrum* L. B, common; disturbed areas; Jan–Apr.
 **Raphanus sativus* L. Similar to *R. raphanistrum*.
Rorippa palustris (L.) Bess. subsp. *glabra* (O. E. Schultz) Stuckey. A or B, occasional; disturbed areas; Apr.
 **Sisymbrium officinale* (L.) Scop. A, occasional; disturbed soil near an irrigation ditch; Apr.

Callitrichaceae

- Callitriche hermaphrodita* L. var. *hermaphrodita*. A, occasional; irrigation ditches; Apr.
Callitriche heterophylla (Pursh.) subsp. *bolanderi* (Hegelm.) Calder & Taylor. P, common and widespread in pools, hogwallows, and ditches, less common in vernal marshes; Mar.
Callitriche longipedunculata Morong. A, occasional; hogwallows; Apr.
Callitriche marginata Torr. A, occasional; pools and hogwallows; Apr.

Campanulaceae

- Downingia bella* Hoov. A, abundant; pools, hogwallows, and seeps; Apr–May.
Downingia bicornuta Gray. A; hogwallows, seeps, and pools; Apr–May.
Downingia cuspidata (Greene) Greene. A; pools; May.
Downingia ornatissima Greene. A; seeps, hogwallows, and shallow pools or vernal marshes; Apr–May. This species occurs with *D. bella*, but with *D. bicornuta* at only one location, a wet depression.
Githopsis specularioides Nutt. A, uncommon; upland; Apr.

Caryophyllaceae

- **Cerastium glomeratum* Thuill. A, widespread on upland, and common in disturbed areas; Mar–Apr.
Minuartia californica (Gray) Mattf. [*Arenaria californica* (Gray) Brew.] A, common; thin soils and cobbled areas of Tuscan loam, and especially in dried hogwallows; Feb–May.
Paronychia ahartii Ertter. A; small population found on thin soil of well-drained upland at northeast corner of Preserve; Mar–Apr.
 **Petrorhagia velutina* (Gussone) Ball & Heywood. [*Tunica prolifera* L., *Kohlrauschia velutina* (Guss.) Reichenb.] A, common; upland or less moist seeps; Apr.
 **Sagina apetala* Ard. A; dried thin or rocky soil of disturbed areas; Apr.
Sagina decumbens (Ell.) T. & G. subsp. *occidentalis* (Wats.) Crow. [*S. occidentalis* Wats.] A, common; scattered in low or disturbed areas of Tuscan loam or deeper soils; Apr.
 **Silene gallica* L. A, occasional; disturbed areas; Apr.
 **Spergularia bocconii* (Scheele) Foucaud. A, occasional; disturbed areas; Apr.
 **Spergularia rubra* (L.) J. & C. Presl. A; disturbed, low and dried areas; Apr–May.
 **Stellaria media* (L.) Vill. A; disturbed areas; Apr.

Chenopodiaceae

- **Chenopodium vulvaria* L. A; disturbed Tuscan loam; Jul.

Convolvulaceae

- **Convolvulus arvensis* L. P, abundant; disturbed areas, becoming invasive in pools; May–Aug.

Crassulaceae

- Crassula connata* (Ruiz. & Pav.) Berger var. *eremica* (Jepson) Bywater & Wickens [*C. erecta* H. & A.] A; dried hogwallows, outcrops, and thin soil of upland; Feb–Mar.
Crassula saginoides (Maxim.) Bywater & Wickens [*Tillaea drummondii* Torr. & Gray var. *bolanderi* (Wats.) Jepson. A; hogwallows and seeps; Mar–Apr.
 **Crassula tillaea* Lester-Garland [*C. muscosa* (L.) Roth] A; shallow depressions on upland; Tuscan loam; Mar–Apr.
Parvisedum pumilum (Benth.) Clausen. A; outcrops on Tuscan soils; Apr–May.

Cuscutaceae

- Cuscuta howelliana* Rubtsoff. A, uncommon; hogwallows and shallow, dried pools; parasitic on *Navarretia leucocephala*, *Boisduvalia cleistogama*, *Eryngium vaseyi* var. *vallicola*, and *Downingia* species; May–Jun.

Elatinaceae

- **Elatine heterandra* Mason. A, common; wet mud and sand of seeps; May–Jun.

Euphorbiaceae

- Chamaesyce glyptosperma* (Engelm.) Small. [*Euphorbia glyptosperma* Engelm.] A; found at one site: disturbed soil near an irrigation ditch at crossing under Highway 99; Jun.
Chamaesyce hooveri (Wheeler) Burch. [*Euphorbia hooveri* Wheeler] A, rare; dried vernal pools; Jun–Sep.
 **Chamaesyce maculata* (L.) Small [*Euphorbia maculata* L.] A; found in a hogwallow on Tuscan loam; Aug.
Chamaesyce ocellata (Dur. & Hilg.) Millsp. [*Euphorbia ocellata* Dur. & Hilg.] A, common; pools, hogwallows, or flat upland; Jul–Oct.
Eremocarpus setigerus (Hook.) Benth. A, ubiquitous; dried vernal pools and flat upland; thin Tuscan or clay loam; Jun–Aug.

Fabaceae

- Astragalus gambelianus* Sheld. A, occasional; upland; Tuscan or deeper soil; Mar–Apr.
Astragalus pauperculus Greene. A, rare; thin soil of well-drained Tuscan upland; Mar–Apr.
Lupinus bicolor Lindl. subsp. *pipersmithii* (Heller) D. Dunn. A; upland, drained sites or shallow hogwallows; thin Tuscan or deeper soils; Mar–Apr.
Lupinus nanus Dougl. in Benth. subsp. *apricus* (Greene) Ell., Hard., & Mank. [*L. vallicola* Heller subsp. *apricus* (Greene) D. Dunn.] A; upland; Tuscan loam; Mar–Apr.
Lupinus polycarpus Greene. A; upland; Tuscan loam; Mar–Apr.
Lupinus subvexus C. P. Sm. A, occasional; low areas of Anita clay; Apr–May.
 **Medicago polymorpha* L. var. *polymorpha*. A, common; upland, edges of hogwallows, pools, and outcrops; Mar–Apr.
 **Medicago polymorpha* L. var. *brevispina* (Benth.) Heyn. A; with var. *polymorpha*; Mar–Apr.
Trifolium albobpurpureum T. & G. A, occasional; upland; Tuscan loam; Apr–May.
Trifolium amplexens T. & G. A, common; Tuscan loam or deeper soils; Apr–May.

Trifolium depauperatum Desv. A, abundant; flat or drained areas of upland; Tuscan or deeper soils; Mar–Apr.

**Trifolium fragiferum* L. P; damp edges of irrigation ditches and disturbed areas; Mar–Apr.

**Trifolium hirtum* All. A; upland; thin, baked Tuscan loam or clay loam; Apr–May.

Trifolium microcephalum Pursh. A, uncommon; Tuscan loam; May.

**Trifolium repens* L. P; damp areas along irrigation ditches; Jun–Jul.

Trifolium tridentatum Lindl. var. *tridentatum*. A; upland or less moist areas of seeps; Tuscan loam or deeper soils; Apr–May.

Trifolium variegatum Nutt. A; edges of irrigation ditches; Apr–May.

Gentianaceae

Centaurium floribundum (Benth.) Rob. A; less moist portions of seeps; often forms a zone between more typical seep species and those of dry upland; Jun–Aug.

Centaurium venustum (Gray) Rob. subsp. *abramsii* Munz. A; open, flat upland; Tuscan or Keefers loam; Jun–Jul.

Cicendia quadrangularis (Lam.) Griseb. A; open flats of upland, and depressions; Mar–Apr.

Geraniaceae

**Erodium botrys* (Cav.) Bertol. A, common outside of wettest areas; Feb–Apr.

**Erodium brachycarpum* (Godr.) Thell. [*E. obtusiplicatum* (Maire, Weiller & Wilcz.) T. J. Howell] A, abundantly weedy outside of wettest areas; Mar–May.

**Erodium cicutarium* (L.) L'Her. A, less common than *E. brachycarpum*; upland in disturbed areas but outside of wettest parts; Feb–Apr.

**Erodium moschatum* (L.) L'Her. A, least common *Erodium* species; disturbed areas; Apr–May.

**Geranium dissectum* L. A, occasional on upland, more common near seeps or vernal pools on deeper soil; Apr–Jun.

Hydrophyllaceae

Nemophila pedunculata Dougl. ex. Benth. A; upland; thin Tuscan loam, on fresh soil of pocket gopher mounds; Apr.

Hypericaceae

Hypericum anagalloides Cham. & Schlecht. A, occasional; along edge of irrigation ditch in rich clay loam; Jul.

Lamiaceae

Pogogyne zizyphoroides Benth. A, common in hogwallows, occasional on upland, and later in pools; Apr–May.

Trichostema lanceolatum Benth. A; upland; thin Tuscan loam; Aug–Sep.

Limnanthaceae

Limnanthes douglasii R. Br. var. *rosea* (Hartw. in Benth.) C. T. Mason. A, common; vernal marshes and hogwallows or edges of pools; Feb–Apr.

Lythraceae

Ammannia coccinea Rottb. A; wet mud along irrigation ditches; May–Aug.

Lythrum hyssopifolia L. A, common; wet mud of irrigation ditches; May–Aug.

Malvaceae

**Malva nicaeensis* All. A; disturbed area around barn; Tuscan loam; Jun.

Sidalcea diploscypha (T. & G.) Gray. A, common but widely scattered on upland slopes or near vernal wet flats; May–Jun.

Sidalcea hartwegii Gray ex Benth. A; scattered on upland; Tuscan loam; Apr.

Sidalcea hirsuta Gray. A, occasional along irrigation ditches, sometimes abundant in pools; May–Jun.

Martynaceae

**Proboscidea louisianica* (Mill.) Thell. A, common in larger vernal pools, occasional near irrigation ditches and near barn; Jun–Jul, and in Sep after late rain.

Molluginaceae

**Mollugo verticillata* L. A; edges of drying pools, seeps, and hogwallows, especially where soil is rocky, sandy, or gravelly; late May–Aug.

Onagraceae

Boisduvalia cleistogama Curran. A, common in pools and vernal marshes, occasional in hogwallows; May–Jun.

Boisduvalia densiflora (Lindl.) Wats. A, occasional; seeps; Jun–Aug.

Boisduvalia glabella (Nutt.) Walp. A, occasional; small pools and hogwallows; Jun–Jul.

Boisduvalia stricta (Gray) Greene. A, common; seeps, hogwallows, and edges of pools; Apr–May.

Clarkia purpurea (Curt.) Nels. & Macbr. subsp. *quadrivulnera* (Doug.) Lewis & Lewis. A, occasional; upland; Tuscan loam; May–Jun.

Ludwigia palustris (L.) Ell. P, occasional; standing water of irrigation ditches; Aug.

Ludwigia peploides (HBK.) Raven. P, common; standing or slowly moving water of irrigation ditches; May–Aug.

Papaveraceae

Eschscholzia lobbii Greene. A, uncommon; upland; Tuscan loam; Mar.

Plantaginaceae

Plantago bigelovii Gray. A; upland, hogwallow or margins of pools, especially on thinner soils; Mar.

**Plantago coronopus* L. A, occasional; Tuscan loam; May.

Plantago erecta Morris. [*P. hookeriana* F. & M. var. *californica* (Greene) Poe.] A, common except in wettest habitats; Mar–Apr.

**Plantago lanceolata* L. P, occasional between dry upland and seep; Jun.

Polemoniaceae

Gilia tricolor Benth. A, common; upland; Tuscan loam or deeper soils; Apr–May.

Linanthus bicolor (Nutt.) Greene. A, common; upland; Tuscan loam; Mar–Apr.

Navarretia heterandra Mason. A; upland; low but drained Tuscan loam or deeper soils; May.

Navarretia intertexta (Benth.) Hook. A; low areas; Tuscan loam or deeper soils; May.

Navarretia leucocephala Benth. A, common; hogwallows, pools, and vernal marshes; Mar–Jun.

Navarretia nigellaeformis Greene. A; found at only one site on Tuscan loam; May.

Navarretia pubescens (Benth.) H. & A. A; scattered on upland; Tuscan loam; May–Jun.

Navarretia tagetina Greene. A; scattered on upland; Tuscan loam; May–Jun.

Polygonaceae

Chorizanthe polygonoides T. & G. A; upland; thin Tuscan loam; Apr–May.

**Polygonum aviculare* L. A; upland; disturbed Tuscan loam; Jun–Sep.

Polygonum californicum Meissn. A; upland; disturbed Tuscan loam; Jun.

Polygonum hydropiperoides Michx. var. *asperifolium* Stanf. P; bordering seeps; May.

**Rumex crispus* L. P, becoming common on disturbed sites of upland and seeps, and invading some pools; May–Jun.

Portulacaceae

Calandrinia ciliata (R. & P.) DC. var. *menziesii* (Hook.) Macbr. A, occasional; drained or seep habitats; Mar.

Claytonia perfoliata Willd. [*Montia perfoliata* (Donn.) Howell var. *perfoliata*] A; a damp, disturbed site on Keefers loam; Apr.

Montia fontana L. subsp. *amphoritana* Sennen. [*H. hallii* (Gray) Greene] A; vertical north surface of exposed fanglomerate near an irrigation ditch; Mar–Apr.

Montia linearis (Doug.) Greene. A; a large, shallow hogwallow; Anita clay; Mar.

**Portulaca oleracea* L. A, occasional; margins of pools or in hogwallows; Jul.

Primulaceae

**Anagallis arvensis* L. A; hogwallows, vernal marshes, and margins of ditches on moist soil; Mar–Apr.

Anagallis minima (L.) Krause. A; seeps and pool margins; May.

Dodecatheon clevelandii Greene subsp. *patulum* H. J. Thomps. P, abundant; upland; Tuscan loam; Jan–Mar.

Ranunculaceae

Delphinium variegatum T. & G. f. *emiliae* (Greene) Ewan. P; upland; Tuscan loam; Mar–Apr.

Myosuros minimus L. var. *filiformis* Greene. A; hogwallows; Mar–Apr.

Myosuros minimus L. subsp. *apus* (Greene) Campb. var. *sessiliflorus* (Huth.) Campb. A; scattered in low places; Apr.

Ranunculus aquatilis L. var. *hispidulus* E. Drew. P, common; irrigation ditches; Mar–Apr.

**Ranunculus muricatus* L. A, common on moist banks of ditches, scattered in low vernal wet areas; Apr.

Ranunculus occidentalis Nutt. var. *eisenii* (Kell.) Gray. P, occasional between seep and upland; Tuscan loam; Jun.

Ranunculus pusillus Poir. A; seeps; May.

**Ranunculus sceleratus* L. A, uncommon; along irrigation ditches; Apr.

Rosaceae

Alchemilla occidentalis Nutt. A, occasional; upland; thin Tuscan or deeper soils; Mar.

Rubiaceae

**Galium aparine* L. A; found at one site, on disturbed Tuscan loam; Jul.

Saxifragaceae

Saxifraga nidifica Greene. A, occasional on upland slopes; Mar.

Scrophulariaceae

**Dopatrium junceum* (Roxb.) Buch.-Ham. in Benth. A; standing or slow-moving water of irrigation ditches; Jul.

Limosella acaulis Ses. & Moc. A, abundant; mud or deeper water of irrigation ditches; May.

Lindernia dubia L. var. *anagallidea* (Michx.) Cooperider. A; mud of irrigation ditches; Aug.

Mimulus guttatus Fisch. ex DC. A or P, common in seeps, less common at margins of pools; Apr–Aug.

Mimulus tricolor Hartw. ex Lindl. A; hogwallows and margins of pools; Tuscan loam or deeper soils; Apr.

Orthocarpus attenuatus Gray. A; upland; Tuscan loam; Mar–Apr.

Orthocarpus erianthus Benth. A, abundant; upland; Feb–Apr.

**Verbascum blattaria* L. B or P; found at one site, on disturbed soil; Jul.

Veronica peregrina L. subsp. *xalapensis* (HBK.) Penn. A, abundant; seeps, hogwallows, and vernal marshes; Mar–May.

**Veronica persica* Poir. A; found at one site, on disturbed soil; Mar.

Solanaceae

Physalis angulata L. var. *lanceifolia* (Nees) Waterfall. A, occasional; upland; Tuscan loam; Jul–Sep.

Violaceae

Viola douglasii Steud. P, occasional; upland; Mar.

Zygophyllaceae

**Tribulus terrestris* L. A, uncommon; disturbed sites; Jul–Sep.

ANTHOPHYTA—MONOCOTYLEDONEAE

Alismataceae

Alisma triviale Pursh. P; in a few places in seeps, standing water of irrigation ditches; Jul–Aug.

Echinodorus rostratus (Nutt.) Engelm. A, occasional; sandy mud of seeps along irrigation ditches; Aug.

Sagittaria calycina Engelm. P, occasional; seeps of irrigation ditches; Aug.

Amaryllidaceae

Allium amplexans Torr. P, abundant; upland; Apr.

Brodiaea californica Lindl. P, common; upland, including minor drainages, near seeps, and in thin, gravelly or disturbed soil; May–Jun.

Brodiaea coronaria (Salisb.) Engler. P, occasional; upland; May.

Brodiaea elegans Hoover. P, common; well-drained upland sites; May.

Brodiaea minor (Benth.) S. Wats. P, abundant; thin soils; Apr–May.

Dichelostemma multiflorum (Benth.) Heller. [*Brodiaea multiflora* Benth.] P, common and widespread; Apr–May.

Dichelostemma pulchellum (Salisb.) Heller. [*Brodiaea pulchella* (Salisb.) Greene] P, common; Mar.

Triteleia hyacinthina Greene. [*Brodiaea hyacinthina* (Lindl.) Baker] P, common; Tuscan or deeper soils; Apr. Some specimens appear to be intermediate between this species and *T. lilacina*; there are no clearcut differences in habitat.

Triteleia laxa Benth. [*Brodiaea laxa* (Benth.) Wats.] P, common; upland; Apr–May.

Triteleia lilacina Greene. [*Brodiaea hyacinthina* (Lindl.) Baker var. *greeni* (Hoov.) Munz.] P; Anita clay loam. Phenology as for *T. hyacinthina* (see for comments).

Cyperaceae

**Cyperus difformis* L. A, occasional along seeps; Jul.

Cyperus eragrostis Lam. P, common along seeps; May–Jun.

Cyperus niger R. & P. var. *capitatus* (Britton) O'Neill. P, occasional along seeps; Jun–Jul.

Cyperus strigosus L. P; seeps; Jun–Jul.

Eleocharis acicularis (L.) R. & S. P; seeps; Jun–Jul.

Eleocharis bella (Piper) Svenson. A; seeps; May–Jun.

Eleocharis macrostachya Britton. P, abundant along seeps and margins of some pools (does not flower in the latter); Apr.

Scirpus acutus Muhl. P, occasional along ditches; not seen to flower.

**Scirpus mucronatus* L. P; seeps; Jul.

Juncaceae

Juncus acuminatus Michx. f. *sphaerocephalus* Herm. A or P; margins of irrigation ditches in rich, clay loam; May–Jun.

Juncus balticus Willd. P; habitat as for *J. acuminatus*; May.

Juncus bufonius L. A; seeps and margins of pools and hogwallows; May.

Juncus dubius Engelm. P, occasional; margins of irrigation ditches in rich, clay loam; Jul.

Juncus uncialis Greene. A, uncommon; hogwallows, seeps, and pools; Apr.

Lilaeaceae

Lilaea scilloidea (Poir.) Haum. A, common; seeps, emergent in ditches or drainage of pools; May–Jun.

Liliaceae

Calochortus luteus Doug. ex Lindl. P, uncommon; upland; Tuscan loam; Apr.

Chlorogalum angustifolium Kell. P; upland; Tuscan loam, clay, or Keefers loam; Apr–May.

Chlorogalum pomeridianum (DC.) Kunth. P, occasional; upland; May–Jun.

Fritillaria pluriflora Torr. in Benth. P; occasional populations on upland, heavier clay soils and nearly always in association with *Zigadenus fremontii*; Mar.

Odontostomum hartwegii Torr. P, common; upland; Tuscan loam or deeper soils; May.

Zigadenus fremontii Torr. P, abundant; low areas of upland in heavier soils; Feb–Mar.

Poaceae

**Agrostis avenacea* Gmel. A, occasional; upland; May–Jun.

**Aira caryophyllea* L. A; upland; Mar–Apr.

Alopecurus carolinianus Walt. A, occasional; upland; May.

Alopecurus saccatus Vasey. A; vernal marshes, pools, and hogwallows; Mar–Apr.

Aristida oligantha Michx. A; upland; Jul.

**Avena barbata* Brot. A, common; upland or flat places; Mar–Apr.

**Avena fatua* L. A, uncommon; upland; Apr–May.

**Briza minor* L. A; upland; Apr–May.

**Bromus diandrus* Roth. A; upland; Mar–Apr.

**Bromus madritensis* L. A, occasional; upland; May.

**Bromus mollis* L. A, common; widespread but infested with smut where invading small pools; Mar–Apr.

**Bromus rubens* L. A, common; upland; Mar–Apr.

**Crypsis schoenoides* (L.) Lam. [*Heleochoa schoenoides* L.] A; margins of pools, vernal marshes; Jun.

**Crypsis vaginiflora* (Forsk.) Opiz. [*C. niliaca* Fig. & DeNot.] A; habitat similar to *C. schoenoides*; Jul.

**Cynodon dactylon* (L.) Pers. P, common in disturbed areas; Apr.

- Deschampsia danthonioides* (Trin.) Munro ex Benth. A, common; hogwallows, small pools, and vernal marshes; Apr.
- Diplachne fascicularis* (Lam.) Beauv. [*Leptochloa fascicularis* (Lam.) Gray] A, abundant; seeps; Jun–Jul.
- **Echinochloa colonum* (L.) Link. A, abundant; seeps; Jul.
- **Echinochloa crusgalli* (L.) Beauv. var. *crusgalli*. Similar to *E. colonum*.
- **Echinochloa crusgalli* (L.) Beauv. var. *oryzicola* (Vasing) Ohwi [*E. oryzicola* (Vasing) Vasing] Occasional; seeps; phenology as for *E. colonum*.
- **Eragrostis cilianensis* (All.) E. Mosher. A, abundant; seeps; Jul.
- **Gastridium ventricosum* (Gouan) Schinz. & Thell. A; upland or hogwallows; May.
- **Hordeum geniculatum* Allioni. [*H. hystrix* Roth.] A; upland or seep; Tuscan loam; Apr–May.
- **Hordeum leporinum* Link. A; upland, especially disturbed areas; Apr–May.
- **Koeleria phleoides* (Vill.) Pers. A; upland, especially outcrops; Apr–May.
- **Lolium multiflorum* Lam. P, common; upland or seep; Apr–May.
- **Lolium perenne* L. P; upland or seep; Jun.
- Melica imperfecta* Trin. A, uncommon; upland; Apr.
- Orcuttia pilosa* Hoover. A, rare; dried vernal pools; abundant in large pools; Jun–Jul.
- Orcuttia tenuis* Hitchc. A, rare; dried vernal pools; found in one pool, where it was abundant; May, or Jul after late rain.
- Panicum dichotomiflorum* Michx. A, common; muddy margins of irrigation ditches; Jun–Jul.
- **Paspalum dilatatum* Poir. P; mud or standing water of irrigation ditches; Jun–Jul.
- Paspalum paspaloides* (Michx.) Scribn. [*P. distichum* L.] P; muddy margins of irrigation ditches; Jun.
- **Phalaris paradoxa* L. A; upland; Tuscan loam or deeper soils; May.
- **Poa annua* L. A; upland, outcrop, and shallow pools and hogwallows; Mar–May.
- Poa scabrella* (Thurb.) Benth. ex Vasey. P, occasional; Anita clay; May.
- Poa tenerrima* Scribn. P; upland, especially near or in hogwallows; Tuscan loam; Mar–Apr.
- **Polypogon interruptus* HBK. P; found at one site, near a seep on Tuscan loam; May.
- **Polypogon maritimus* Willd. A, common; damp areas near irrigation ditches; Tuscan or Keefers loam; May.
- **Polypogon monspeliensis* (L.) Desf. A, common near seeps and in hogwallows; Tuscan loam or deeper soils; May.
- Scribneria bolanderi* (Thurb.) Hack. A, occasional; Tuscan loam; Apr.
- **Sorghum halapense* (L.) Pers. P, occasional; gravelly areas; Jun.
- Stipa pulchra* Hitchc. P, occasional on upland Tuscan loam, more common on deeper, clay soils; Apr–May.
- Tuctoria greenei* (Vasey) J. Reeder [*Orcuttia greenei* Vasey] A, rare; dried vernal pools; common but not abundant in pools on Preserve; Jul.
- **Taeniattherum caput-medusae* (L.) Nevski. [*T. asperum* (Simonkai) Nevski, *Elymus caput-medusae* L.] A; scattered on upland, especially disturbed areas; Tuscan loam or Anita clay; May.
- **Vulpia bromoides* (L.) S. F. Gray [*Festuca dertonensis* (All.) Asch & Graebn.] A; upland or near seep or hogwallow; Tuscan loam; Apr.
- Vulpia microstachys* (Nutt.) Benth. var. *ciliata* (Beal) Lonard & Gould. [*Festuca eastwoodae* Piper] A, common; well-drained upland; Apr.
- Vulpia microstachys* (Nutt.) Benth. var. *confusa* (Piper) Lonard & Gould. [*Festuca confusa* Piper] A, common; thin soils of upland; Apr.
- **Vulpia myuros* (L.) K. C. Gmelin var. *hirsuta* Hack. [*Festuca megalura* Nutt.] A, common; upland; Tuscan or deeper soils; Mar–Apr.
- **Vulpia myuros* (L.) D. C. Gmelin var. *myuros* [*Festuca myuros* L.] A, common; similar to *V. myuros* var. *hirsuta*; Mar–Apr.

Potamogetonaceae

Potamogeton diversifolius Raf. P; slow-moving water of irrigation ditches; May.

Typhaceae

Typha angustifolia L. P, occasional; irrigation ditches; Jun.

Typha latifolia L. P, occasional; irrigation ditches; Jun.

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SOLIVA (ASTERACEAE: ANTHEMIDEAE) IN CALIFORNIA

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ABSTRACT

Soliva sessilis, *S. pterosperma*, and *S. daucifolia* have been distinguished from each other on achene characteristics and habitat, and have been listed as members of the naturalized flora of California. Examination of over 310 collections from California documented a continuum of achene morphology and an indiscriminate distribution of morphs that form a single taxonomic species. Synonymy of *S. sessilis* also is extended to include *S. neglecta* and *S. valdiviana*.

Soliva Ruiz Lopez & Pavon is a genus of low growing annuals first described in 1794 from Chile. Native to South America, it was naturalized in California by 1836 when Nuttall visited Santa Barbara and collected what he later (1841) described as *S. daucifolia*. *Soliva* may have come to California from Chile in shipments of hides (Cabrera 1949, Healy 1953), but probably not on livestock (Raven 1963).

Achenes of *Soliva* are well adapted for long-distance dispersal, as suggested by their unique morphology. They are small and light-weight with stiff, appressed pubescence, and disperse by adhering to animals or other objects that move. More importantly, however, they have a sharp, persistent stylar spine that easily becomes imbedded in dispersal agents. *Soliva* is found most often in hard-packed soil or near well-beaten paths or roadsides. In addition, it is found in planted lawns. Human activities are probably a major means of dispersal for *Soliva*, which occurs mainly in areas with large human populations or along major travel routes. *Soliva* spp. are adventive and have become established world-wide in many such locations.

Soliva sessilis, *S. pterosperma*, and *S. daucifolia* have been recognized for California (Crampton 1954), although two other species, *S. neglecta* and *S. valdiviana*, could be recognized based on published descriptions by Cabrera (1949) and Philippi (1864–65). This group of species was called subgenus *Eusoliva* (= *Soliva*; see Voss et al. 1983) by Cabrera (1949) and includes about half of the genus. The remaining five species do not occur in North America and differ markedly from the species considered here in both achene and vegetative characters (Cabrera 1949). Cabrera (1949) treated *S. daucifolia* as a synonym of *S. sessilis*, and distinguished between it and the remaining species only by means of achene characters. Crampton

(1954) distinguished between *S. sessilis*, *S. pterosperma*, and *S. daucifolia* by achene characters and habitat. All published descriptions for the five taxa are basically identical with regard to vegetative and floral morphology; both kinds of characters are deemphasized because they are not used to distinguish the species. Floral morphology is of limited use as a descriptive or distinguishing character because of the short duration and minute size of the flowers.

The generally accepted (Cabrera 1949, Crampton 1954, Munz 1959) achene morphologies that characterize the five taxa under discussion are illustrated in Fig. 1 (A–E). Achenes of *S. sessilis* are pubescent and have wide, entire wings that usually have large wing-tips. Achenes of *S. pterosperma* are pubescent and have wide wings, long, tapering, curved tips, and a large sinus between upper and lower wing-lobes that is positioned about one-third of the distance from the base to the top of the wing (excluding the wing-tip). Achenes of *S. daucifolia* are pubescent, have no wings, but have small wing-tips. Those of *S. neglecta* are similar to those of *S. sessilis*, except they are glabrous rather than pubescent. *Soliva valdiviana* usually includes plants with wingless, wing-tipless, glabrous achenes (Cabrera 1949), but Philippi's (1864–65) original description does not specifically mention a lack of pubescence and refers to the presence of wing-tips. Notes on many specimens of *Soliva* suggest that the achene characters are unreliable. This paper presents an examination of *Soliva* collections from California to determine the species present, and a study of achene and general morphology to review the distinguishing characteristics for the species considered.

MATERIALS AND METHODS

To examine achene and vegetative morphology and determine which species of *Soliva* occur in California, I studied over 250 specimens from CAS, CHSC, DS, JEPS, POM, RSA, and UC. I also made 60 collections of *Soliva* in various parts of the state. A list of specimens examined in this study is included in Ray (1984), which is available at Stanford University and CAS.

Some terms used in this paper relative to achene morphology are illustrated in Fig. 1 (F–R). Wing-tips are usually pointed projections that occur in pairs on either side of the central stylar spine (see Fig. 1 and below), and often the outside edges are continuous with those of the wing. The wing is a region flattened in the plane of the achene that occurs on either side of the achene. The stylar spine, derived from the persistent style, arises from the center of the achene and is continuous with the central, thicker body of the achene. A sinus is a region where the edge contour of the wing is broken sharply, like a “bite” out of the wing, or sometimes appears as a crack. An incurved region of the wing is a kind of sinus with a very

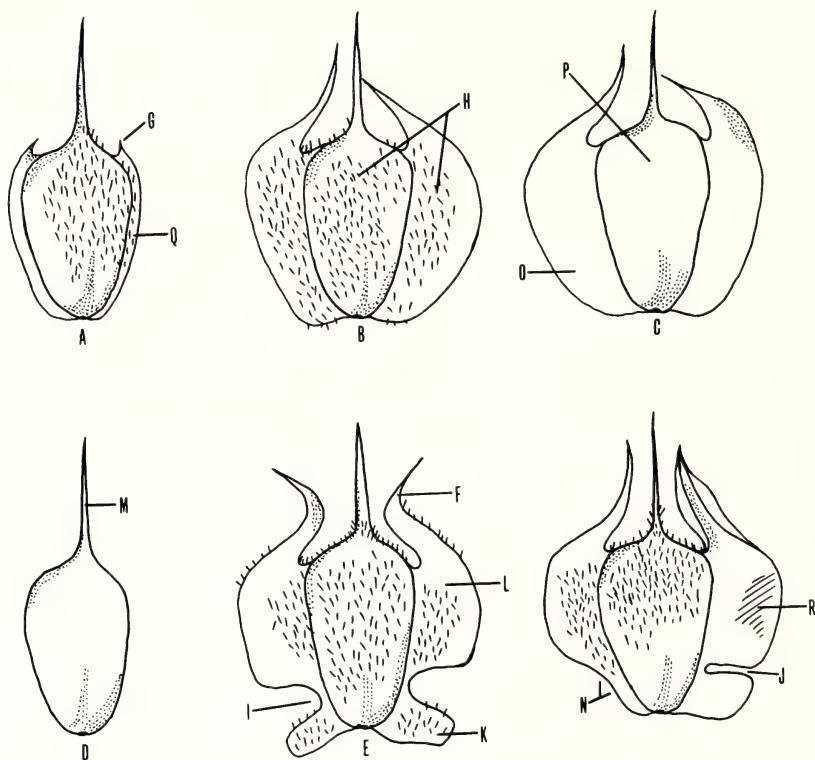


FIG. 1. Achene morphologies for five "taxa" of *Soliva* (after Cabrera 1949, Crampton 1954). A. *S. daucifolia*. B. *S. sessilis*. C. *S. neglecta*. D. *S. valdiviana*. E. *S. pterosperma*. Morphological terms used in the text: F. Long wing-tip. G. Short wing-tip. H. Typical short, stiff, appressed pubescence on achene "body" and wings. I. Sinus. J. Narrow sinus. K. "Below" (lower lobe). L. "Above". M. Stylar spine. N. Incurved region of wing. O. Wing entire. P. Achene "body" (in this case glabrous). Q. Narrow wing (=margin). R. Hyaline area of wing (thin and transparent).

shallow, smooth interruption of the wing edge contour.

Although vegetative morphology has not been used in the literature to distinguish the species of *Soliva* under consideration here, I examined vegetative characters in view of possible relationships to achene characters. These characters included typical habit and size of plants; leaf position, shape, divisions, surface texture, and pubescence; internode characters; and aspects of the inflorescence.

I examined achenes from each collection by stereoscope. One or more (depending on variation occurring on sheet) representative achenes were drawn in detail and described. Achene body and total length were measured, because this character has been used to recognize *S. daucifolia* (Crampton 1954). Vegetative characteristics from

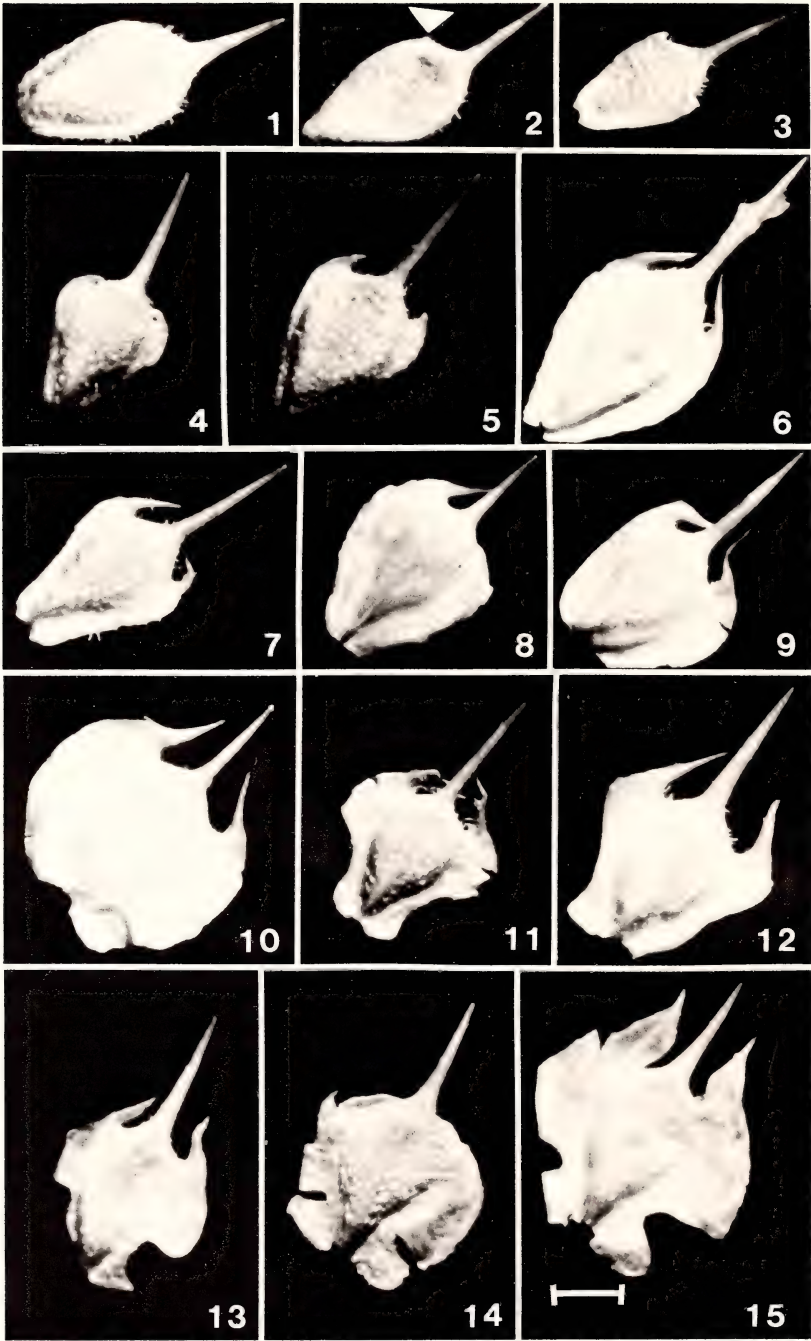
each collection were described. Based on the accumulated data, 15 achene morphology categories (Fig. 2) were designated, each represented by a specimen. I then assigned all specimens to one or more (depending on variation) of these morphological categories.

The range of *Soliva* achene variation is described here by reference to the above mentioned series of 15 numbered, artificial achene morphs. The features of each morph are described in detail in the caption for Fig. 2. Although the artificial morphs are discrete, many further intermediates occur, and in fact every achene is somewhat unique. The morphs are not necessarily spaced equally over the range of variation. Some morphs are of more general form than others, and thus contain more internal variation (intermediates) and represent more collections. Achene morphology was not always uniform in a particular collection and I noted many cases in which variation occurred on individual plants or even within capitulae. The generally recognized species (Cabrera 1949, Crampton 1954) correspond approximately with the artificial achene morphs (Fig. 2) as follows: *S. valdiviana*, morphs 1–2; *S. daucifolia*, morphs 4–6; *S. sessilis*, morphs 9–10; and *S. pterosperma*, morphs 13–15. *Soliva neglecta* is found among *S. sessilis* morphs. In the following text, the phrase “achene morph” or “achene morph number” refers to an actual observed morphology corresponding to that particular numbered artificial morph from Fig. 2.

RESULTS AND DISCUSSION

Achene morphology. Achenes in all specimens have a central portion or “body” of more or less similar shape, including a sharp, persistent stylar spine (Fig. 1P), and most also have wings of various shapes and sizes, and/or wing-tips. A few achenes are wingless and wing-tipless. A carina on the achene body toward the base on the convex (abaxial) side is usually more pronounced in the drier collections from late in the season. Achenes and their appendages vary in color from light green or tan to dark brown. They vary in the distribution of typically short, stiff, appressed pubescence, and often have minute purple spots variously distributed on the body, stylar spine, and wings. The achene body is usually bilaterally symmetrical, but the two wings and wing-tips sometimes differ from one another in shape and size. Wings vary in shape, width, thickness, and edge characters, such as splits, cracks, and sinuses. Some wings are translucent or hyaline in limited regions. Wing-tips vary in width, length, curvature, and degree of furcation (Figs. 1, 2). Wing-tips on a given achene are sometimes dissimilar.

Total achene length varies from 3.5–5.2 mm. Crampton (1954) reported that *S. daucifolia* had achenes with consistently shorter



bodies than those of either *S. sessilis* or *S. pterosperma*. I observed no consistent relationship between achene body length and a particular achene morphology. Achene body length appeared to vary with overall length.

I observed no consistent relationship of any vegetative character or group of such characters to any achene character. In fact, vegetative morphology was relatively uniform in all specimens. Some previously unreported minor details of habit and leaf morphology were observed, and I have included these in the description below (compare with Cabrera 1949, Munz 1959).

A number of specimens that I examined corresponded with the description (with illustration) of *S. neglecta* Cabrera [e.g., *Bacigalupi* 1527 (DS), *Breedlove* 4405 (DS), *Cerrate* 2515 (UC), *Eastwood and Howell* 2561 (CAS), *Knight* 626 (CAS), *Mason* 4315 (DS), and *Raven* 19734 (DS, RSA)]. Achenes from these specimens also usually matched the generalized morphology of *S. sessilis* (Fig. 1), but are glabrous or nearly so. This condition also was found in other col-

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FIG. 2. Achene variation in *Soliva sessilis*. Achenes shown are from representative collections that are cited below and that form the basis for artificial achene morphs, which describe the range of wing and wing-tip variation. Morphs are numbered 1–15, and are followed by a description and citation. Compare with Fig. 1, A–E. Note that each artificial morph contains internal variation; as discussed in the text, some artificial morphs are circumscribed more broadly in terms of actual achene variation, than others. Morphs are in a proposed order of complexity of wing and wing-tip features. Scale in mm is shown with morph 15.

1. Achenes with no wings, no wing-tips; *Wiggins* 12352 (DS). 2. No wings, vestigial tips; *Tracy* 6684 (UC). 3. Wings vestigial above, no tips; *Raven* 10668 (CAS). 4. Wings narrow above, absent below, tips evident; *Eastwood* 143 (UC). 5. Wings extremely narrow, tips vestigial to evident; *Linsdale s.n.* (CAS). 6. Wings to 0.25 mm wide, tips longer than in #5; *Raven* 6933 (CAS). 7. Wings wider above, smoothly curving to narrow below, or slightly lobed below; *Howell* 41480 (CAS). 8. Wings of medium width, about halfway (ca. 0.75 mm wide) between narrow (#5) and wide (#9, 10, and beyond) with many edge and tip variations. May be incurved below; *Eastwood and Howell* 2561 (CAS). 9. Wings 1 mm or more wide, rounded, tips long with a number of variations; *Lee and Mason* 9105 (UC). 10. Wings wide, more or less rounded with many edge and tip variations; *Howell* 42163 (CAS). 11. Wings wide above, narrower below, with the upper lobes curving into the lower, but the lower not protruding beyond the edge line once it is vertical such that a sinus is not formed; *Howell* 29811c (CAS). 12. Wings wide above, curving to small sinuses below, blending into small lobes that protrude below these, the lobes not as wide as the wings above; *Jepson* 18856 (JEPS). 13. Wings wide above and about the same below, divided by a sinus that is wide and fairly deep. Contour of upper and lower lobes more or less continuous; many edge and tip variations; *Raven* 6624 (CAS). 14. Wings wide above, about the same or less below, divided by a relatively narrow sinus that is quite deep. Contour of upper and lower lobes more or less continuous; *Jepson* 18018 (JEPS). 15. Wings wide, upper lobes wider than the lower, divided by a deep sinus, entire achene rather arrowhead-shaped, the contour of upper and lower lobes not continuous; *Hoover* 1996 (JEPS).

lections that exhibited different morphologies [e.g., *Ashwin 535* (CAS), *Howell 45554* (CAS), *Jepson 11563* (JEPS), *Ray 33* (DS), and *Thomas 7101* (DS)]. Glabrous achenes are found occasionally throughout the range of wing-character morphology. Degree and distribution of pubescence also varies over that range. *Howell 45554* has both pubescent and glabrous achenes, but not on the same plant. Thus, pubescence and wing morphology appear to vary independently. In view of this variability, the distinction between *S. sessilis* and *S. neglecta* is unclear.

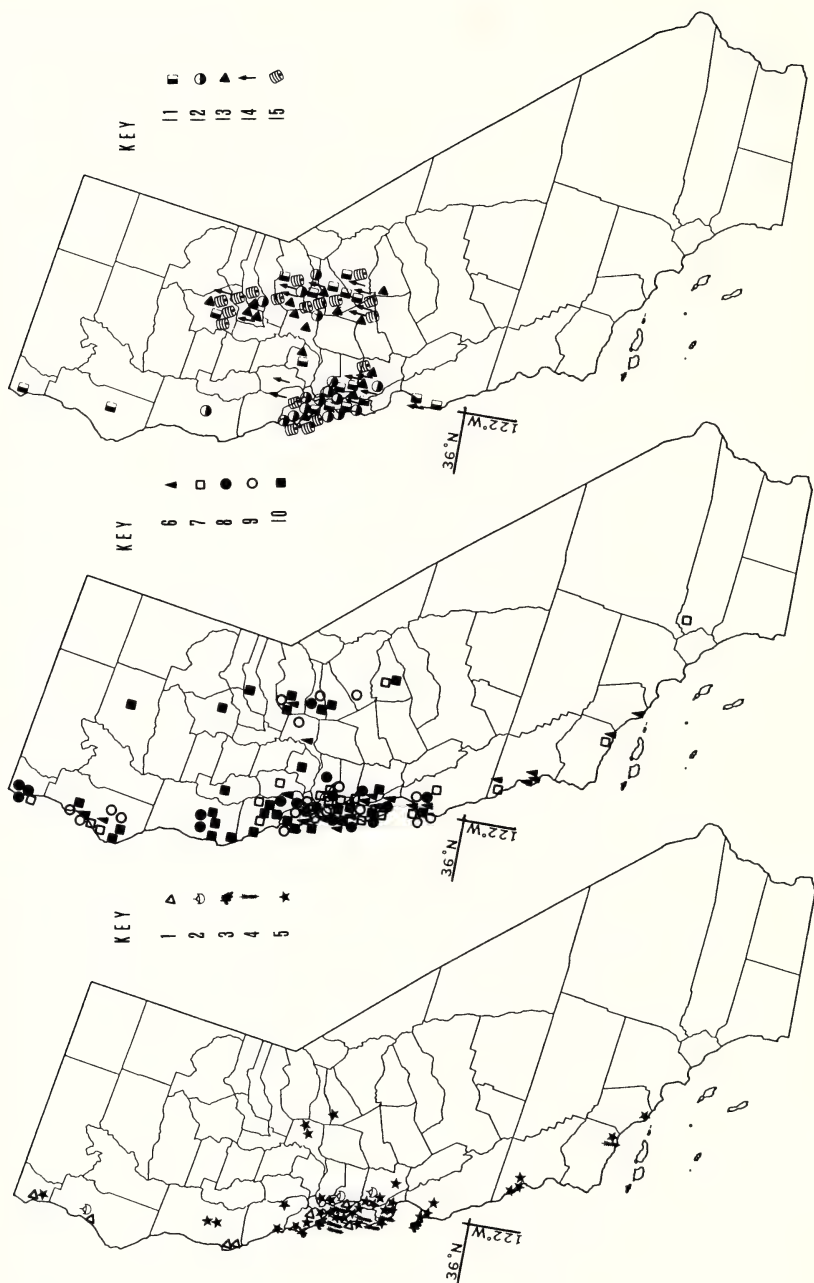
The description of *S. valdiviana* (Philippi 1864–65) includes no specific reference to presence or lack of achenal pubescence, so it corresponds with a number of the specimens examined in this study [e.g., *Ashwin 535* (CAS), *Howell 21653* (CAS), *Koch 812* (UC), *Rose 39154* (UC), *Tracy 6684* (UC), and *Wiggins 12352* (DS, UC)]. Nuttall (1841) described *S. daucifolia* as “slenderly margined” and “minutely bidentate at the summit”. Philippi (1864–65) described *S. valdiviana* as “haud alatis” (having no wings) and “spinoso coronatis” (spined crown). Cabrera (1949) includes an illustration of *S. valdiviana* that shows no wing-tips. Because the wings have been an important descriptive character in the literature, the assumption that the term “margin” was used by Nuttall (1841) to refer to the wing is a logical one. The descriptions “slender margin” (i.e., very narrow wings) and “haud alatis” (i.e., lacking the wide wings some other achenes have) are not greatly distinct. The descriptions “minutely bidentate at the summit” and “spinoso coronatis” also are similar; both refer to the small wing-tips that occur in achene morphs 2, 4, and 5 (Fig. 2). Therefore, the original published descriptions for *S. daucifolia* (Nuttall 1841) and *S. valdiviana* (Philippi 1864–65) are similar. Significant variation occurs in wings and wing-tips for artificial morphs 1–5 (Fig. 2), which is the range described for achenes of both *S. daucifolia* and *S. valdiviana*. The distinction between the two taxa is unclear.

The specimens cited by Crampton (1954) to support recognition of *S. daucifolia* differ morphologically from each other and, in some cases, from Nuttall's (1841) description. *Tracy 1089* (UC) has achenes with narrow wings and sinuate edges, often wider above, with long wing-tips; *Rose 39154* (UC) and *Wiggins 12352* (DS, UC) have achenes with no wings and no wing-tips (morph 1, Fig. 2); and *Eastwood 143* (UC) has achenes with the widest portion of the wing above, the wings absent below, and the wing-tips curved sharply inward (obscured behind the stylar spine in Fig. 2). Crampton's (1954) illustration of *Eastwood 143* is similar to achenes I examined, but differs in details of wing morphology. Crampton cited a specimen he called “*Les Koch 812*”, which probably corresponds to *Leo F. Koch 812* (UC). Examples of achene morphs 1–10 were found on this sheet. Crampton (1954) provided illustrations of *Crampton 1121*

and *Crampton 1223*, with no discussion of these in the text. On examination, I found achenes from these specimens to correspond loosely with the illustrations, but they differ substantially in detail. Apparently the achenes examined by Crampton (1954) were different from those seen in the present study, which again suggests taxonomic unreliability in achene characters.

Soliva collections that show variation of achene morphology between plants on the same sheet or within individual plants or capitulae are listed below. Each collection is listed with the artificial achene morph numbers (see Fig. 2) corresponding to achenes found on that sheet. An asterisk indicates variation within the same plant: Alameda Co.: *Lee 701* (JEPS), 5, 7, 8. Amador Co.: *Hansen 1054* (UC), 8, 11, 12, 14*. Butte Co.: *Ahart s.n.* (CAS), 10, 14*. Humboldt Co.: *Davy 5684* (UC), 9, 11*. Mendocino Co.: *Koch 812* (UC), 1–10. Monterey Co.: *Howell 41480* (CAS), 6, 7*. San Mateo Co.: *Abrams 2423* (DS), 6, 10, 14; *Dudley s.n.* (RSA), 11, 12*; *Ferris 4157* (DS), 11, 12, 13*; *Ray 37* (DS), 7, 12*; *Ray 38* (DS), 4, 7, 8*; *Ray 40* (DS), 6, 12*; *Thomas 4283* (DS), 4, 7, 8*. Santa Clara Co.: *Dudley s.n.* (DS), 6, 12; *Thomas 4822* (RSA), 8, 11*. Santa Cruz Co.: *Ray 36* (DS), 6, 7*. Sonoma Co.: *Brandegees s.n.* (POM), 5, 10, 14*. Tuolumne Co.: *Howell 40693* (CAS), 14, 15*; *Johannsen 883* (UC), 9, 11, 15*.

Dispersal. Humans appear to be a major factor in the spread of *Soliva* in its role as an adventive species. It consistently occurs in either hard-packed paths, waste ground, dirt roads, or cultivated lawns. In collecting, I observed that achenes easily became imbedded in my hands. Achenes are probably dispersed on shoes or clothes, or on the tires of cars or other machines. It seems likely that in lawns on the Stanford campus, where *Soliva* occurs frequently and is spreading, achenes are moved on the tires of large lawnmowers. To test the hypothesis that achenes can move in tires, I rode a balloon-tired bicycle through some mature patches of *Soliva* in a lawn, and then checked both tires after about 150 m riding distance. Five achenes were found, two of which were firmly imbedded. This indicates that not only can short distance dispersal occur in tires, but also longer distance movement because the firmly imbedded achenes might remain so for some time. *Soliva*, therefore, is a genus well adapted to dispersal within an area in which the plants are already established, and to locations that may be quite remote. Such new locations are generally in well-travelled areas, where the achenes are most likely to become detached from the dispersal agent and to be pressed into the ground by subsequent traffic. The possibility exists that the distribution pattern in well-travelled and populated areas results from sampling. That is not sufficient reason to discredit overall collection evidence because of the additional strong evidence of



achene dispersal adaptations and the many collections from similar microhabitats.

Distribution. *Soliva* is well established in watered lawns and plantings in many places in California. There are few collections from urban southern California (Los Angeles basin and vicinity), although I have collected *Soliva* in lawns in Santa Monica, Arcadia, Newport Beach, and rural Orange Co., and I have observed it growing in lawns near USC. It is unlikely that the genus is established in many natural or unwatered areas in southern California, because of low seed carryover (Johnson and Lovell 1980) and the relatively long wet period required for growth. In contrast, *Soliva* is probably established in more locations in the San Francisco Bay region and northern California than records indicate.

Distribution maps (Fig. 3) show collection locations for many *Soliva* specimens examined in this study, with a symbol for each indicating an artificial achene morph that corresponded most closely with achenes from that specimen (variation in the same collection not indicated). The three maps are designed to show the distribution of each of the 15 artificial achene morphs. This is necessary because species of *Soliva* have been recognized by alleged localization of particular achene morphologies. Examination of the maps (Fig. 3) may give the impression that achene morphs 11–15 (Fig. 2) occur more often in the Sierra Nevada foothill areas and that morphs 1–6 occur more often on the southern coast. Crampton (1954) made similar observations and used them to support recognition of *Soliva pterosperma* (Sierra foothills) and *Soliva daucifolia* (southern coast). I observed, however, that all achene morphologies were distributed randomly and in high density in the San Francisco Bay region, from which there are more collections than any other region in the state. Also, morphs 5–8 have been collected in the Sierra foothills (Fig. 3). Because of the low frequency of collections in the Sierra foothills and the southern areas (relative to the Bay region), and the random distribution of morphs in the Bay region, localization of particular achene morphologies in the Sierra or southern areas does not seem plausible. Thus, there appears to be no separation of achene morphologies throughout the range of *Soliva* in California.

Conclusion. My observations of achene morphology show that a continuum of variation exists for the achene wing and wing-tip characters in the California collections of *Soliva*. Based on these observations, and the lack of any other consistent variations or major

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FIG. 3. Distribution of *Soliva sessilis* in California. Three maps are provided for clarity in areas of high specimen density. Keys match symbols on maps to artificial achene morph numbers (1–15) in Fig. 2.

separations of habit or habitat, I conclude that only one species of *Soliva* occurs in California. Because this species also occurs in other parts of the world (such as Australia, New Zealand, and South America), and indeed has been introduced into California, this conclusion also applies on a wider basis. By priority of publication, *Soliva sessilis* is the name for this species, and thus the names *S. pterosperma* and *S. daucifolia* are synonyms. The names *S. neglecta* and *S. valdiviana* also appear to be referable to *S. sessilis*.

TAXONOMIC TREATMENT

SOLIVA SESSILIS Ruiz Lopez & Pavon, Syst. Veg. Fl. Per. Chil. 215. 1798.—Type: Chile, “Habitat in plateis et pratis *Conceptionis* (sic) *Chile*, praesertim ad *Mochita*, *Hualpen*, *Andalien* et *Gavilan* tractus”; no specimens seen; description and earlier illustration (Ruiz Lopez & Pavon, Syst. Veg. Fl. Per. Chil. 113, tab. 24, 1794) fix application of the name. See Cabrera (1949) for additional synonymy.

Gymnostyles pterosperma A. L. Juss., Ann. Mus. Natl. Hist. Nat. 4: 262, tab. 61, f. 3. 1804.—*Soliva pterosperma* (A. L. Juss.) Less., Synop. Gen. Compos. 268. 1832.—Type: Argentina, Buenos Aires, “Ex Bonaria. Car. ex sicca in herb. Commers.”, no specimens seen; illustration fixes application of the name. See Cabrera (1949) for additional synonymy.

Soliva daucifolia Nutt., Trans. Amer. Philos. Soc., ser. 2. 7:403. 1841.—Type: California, “. . . within the limits, and in the immediate vicinity of St. Barbara”; no specimens seen; description allows certain application of the name.

Soliva valdiviana Philippi, Linnaea 33:168. 1864–65.—Type: Chile, “Frequens in prov. Valdivia”; no specimens seen; description allows certain application of the name.

Soliva neglecta Cabrera, Notas Mus. La Plata 14:128. 1949.—Type: Argentina, Jujuy, Santa Ana, 3100 m, 29 Feb 1940, *A. Burkart* and *N. S. Troncoso* 11665 (LP; isotype: SI) (not available).

Herbaceous annuals with fibrous roots. Ascending, spindly-stemmed plants to nearly acaulescent plants, or clumpy and compact plants with glomerate leaves and capitulae, or spreading plants with decumbent to prostrate stems and elongate internodes. Compact plants 2–7 cm tall, spreading plants 25 cm diam. Stems 1–10 from base, light- to dark-colored, often purple-spotted, sparsely pubescent to villous. Leaves to 5 cm long, petioled, the bases broad, \pm clasping; once-pinnate, the pinnae with 2–8 \pm palmate narrowly lanceolate lobes, often one lobe smaller, the terminal pinna sometimes single; puberulent to sericeous or villous. Capitulae sessile in axils; disciform; receptacle convex or low-conic; involucre of 5–12 subequal phyllaries, broadly ovate to lanceolate, abruptly acute, in 1–2 series,

2–3 mm long, green to hyaline, pubescent to villous; disc flowers 4–6, perfect, minute, greenish-translucent (yellow stamens within), 4-merous, probably functionally staminate, surrounded by 10–12 naked pistillate flowers. Achenes 3.5–5.2 mm long including stylar spine, the ovate to lanceolate central body \pm carinate, style persistent, becoming hard and sharp, stigmas persistent or deciduous. Achenes wingless (with or without toothlike wing-tips) to wide-winged, the wings thin, opaque to regionally hyaline, the edges notched, incurved, split, cracked, or sinuate; the wing-tips from short, blunt, toothlike projections to long curving tips with thin edges; achenes light green to dark brown, often with minute purple spots, glabrous to variously pubescent. Probably self-fertile. Feb–Jul. Disturbed, hard-packed and weedy areas that receive sufficient water for seed set, especially paths, dirt roads, roadsides, and other well-travelled areas; also in watered lawns.

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ROLE OF FIRE IN THE GERMINATION OF CHAPARRAL HERBS AND SUFFRUTESCENTS

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ABSTRACT

Fifty-seven herbaceous and suffrutescent species common after fire in chaparral were tested for their response to charred wood and heat shock of 120°C for five minutes. Over half of the species germinated readily without either treatment. These included all of the herbaceous perennial monocots, most herbaceous perennial dicots, and a number of annuals. In most species, the heat treatment reduced germination and only one species was stimulated significantly by heat. Forty-two percent of the species showed significant enhancement of germination with charred wood. For some perennials, such as *Penstemon spectabilis* and *Romneya coulteri*, and an annual, *Papaver californicum*, there was a near obligatory requirement for charred wood. Significant enhancement of germination in the presence of charred wood is now known for species in 10 plant families: Asteraceae, Boraginaceae, Brassicaceae, Caryophyllaceae, Hydrophyllaceae, Onagraceae, Papaveraceae, Polemoniaceae, Rubiaceae, and Scrophulariaceae. Several fire-following species, *Eucrypta chrysanthemifolia* and *Dicentra* spp., failed to germinate under any treatment.

Since the early observations of Brandegee (1891), botanists have been impressed by the often spectacular wildflower displays that occur the first growing season after wildfire in chaparral. Over 200 species of annuals, herbaceous perennials, and short-lived suffrutescents have been recorded from chaparral burns. This abundance and diversity of herbs is in marked contrast to the generally depauperate herbaceous vegetation in mature chaparral (Sweeney 1956, Stocking 1966, Keeley et al. 1981).

Nearly all of this temporary vegetation arises from seed or vegetative parts present in the soil prior to burning. This fact has resulted in two theories accounting for the breaking of seed dormancy after fire: 1) seeds are inhibited from germinating by the mature chaparral vegetation (allelopathy) and fire releases seeds from this inhibition, or 2) seed germination is stimulated by fire.

The question of allelopathic inhibition of seeds by chaparral has been examined in numerous studies (Sweeney 1956, McPherson and Muller 1969, Christensen and Muller 1975a,b, Kaminsky 1981, Keeley et al. 1985), but its role in inhibiting seed germination is unclear.

There is strong evidence, however, that many chaparral species have seeds that, under natural conditions, require a stimulus from fire for germination. Germination of some species is stimulated by heat shock from fire that ruptures the seed coat (Sweeney 1956, Christensen and Muller 1975a,b, Keeley et al. 1985). Germination of other fire-following herbs is stimulated by a chemical leached from charred (but not ashed) wood (Wicklow 1977, Jones and Schlesinger 1980, Keeley et al. 1985). Many species have been tested for their germination response to heat shock; however, the vast majority of chaparral herbs and suffrutescents have not been tested for their response to charred wood.

Although germination of many chaparral species is apparently dependent upon one or the other of these fire-related cues, a number of species are known to germinate readily without such cues (e.g., Sweeney 1956, Keeley et al. 1985).

The purpose of this study was to test the germination response of 57 species, representing all of the life-histories and growth forms present in the temporary postfire vegetation. Specific questions addressed were: 1) How widespread is charred wood stimulated germination? 2) For species with charred wood stimulated germination, will heat shock produce a similar stimulation in germination? 3) To what extent can generalizations be drawn concerning the relationship of growth form and germination response?

METHODS

Selection of species was based on availability of plants with mature seed crops that were present in recently burned chaparral. Collections were made between elevations of 500–1500 m in Los Angeles, Riverside, San Diego, San Bernardino and Ventura cos., California. Vouchers have been deposited at LOC (Occidental College). Nomenclature is according to Munz (1974). Seeds of each species were collected from a single population of 25 or more plants during the spring and summer of 1982 and stored in paper bags under room conditions for 14–18 months. Although there is little data on seed longevity of these species, the fact that many species may be absent on a site for decades prior to fire suggests the seed pool in the soil is quite long-lived (Sweeney 1956).

Seeds were sown into 60 × 15 mm petri dishes filled with 15 g (fresh weight) of commercial potting soil (Gro-Lite, see Keeley 1984 for chemical analysis of this soil). Charred wood was made by charring (but not ashing) 1–2 cm diameter stems of the chaparral shrub *Adenostoma fasciculatum* and grinding in a Wiley Mill to pass a 1 mm screen. Charred wood treatments received 0.5 g of this powdered charred wood. For comparison, a heating treatment of seeds was included. The treatment of 120°C for five minutes was selected be-

TABLE 1. GERMINATION OF SELECTED CHAPARRAL HERBS AND SUFFRUTESCENTS IN RESPONSE TO 120°C FOR FIVE MINUTES OR APPLICATION OF POWDERED CHARRED WOOD TO THE GERMINATION MEDIUM (N = 5 DISHES OF 50 SEEDS EACH). A = annual, B = biennial, Hp = herbaceous perennial, S = suffrutescent, * = non-native. # = *Gilia capitata* seeds from two populations were tested, a first year burn and an adjacent mature chaparral stand. ns = no significant difference between treatments ($p > 0.05$); for species with significant difference, treatments with the same superscript are not significantly different at $p > 0.05$.

		Percentage germination				
	Growth form	Control	120°C 5 min	Charred wood	p	
Dicots						
Apiaceae						
	<i>Daucus pusillus</i>	(A)	30	10 ^a	18 ^a	<0.01
	<i>Lomatium dasycarpum</i>	(Hp)	12	1	4	<0.01
Asteraceae						
	<i>Agoseris heterophylla</i>	(A)				
	Beaked achenes		79	86	88	ns
	Non-beaked achenes		62	78	92	<0.001
	<i>Gnaphalium californica</i>	(A/B)	46 ^a	67 ^{a,b}	79 ^b	<0.05
	<i>Heterotheca grandiflora</i>	(A/B)	91 ^a	44	86 ^a	<0.001
	<i>Lactuca serriola</i>	(A*)	53	44	54	ns
	<i>Madia gracilis</i>	(A)	86 ^a	45	86 ^a	<0.05
	<i>Malacothrix clevelandii</i>	(A)	9 ^a	10 ^a	35	<0.001
	<i>Microseris linearifolia</i>	(A)	98	96	95	ns
	<i>Perezia microcephala</i>	(Hp)	35	1	9	<0.001
	<i>Porophyllum gracile</i>	(S)	72 ^a	26	73 ^a	<0.01
	<i>Rafinesquia californica</i>	(A)	4 ^a	3 ^a	55	<0.01
	<i>Stephanomeria virgata</i>	(A)	45 ^a	40 ^a	56	<0.05
Boraginaceae						
	<i>Cryptantha intermedia</i>	(A)	55 ^a	55 ^a	74	<0.05
Brassicaceae						
	<i>Lepidium nitidum</i>	(A)	2 ^a	3 ^a	22	<0.001
	<i>Sisymbrium orientale</i>	(A*)	94	79 ^a	74 ^a	<0.01
	<i>Streptanthus heterophyllus</i>	(A)	1 ^a	7 ^a	25	<0.001
Caryophyllaceae						
	<i>Silene gallica</i>	(A*)	64 ^a	66 ^a	34	<0.01
	<i>S. multinervia</i>	(A)	6 ^a	9 ^a	44	<0.01
Fabaceae						
	<i>Lotus salsuginosus</i>	(A)	6 ^a	24 ^a	2	<0.01
	<i>L. strigosus</i>	(A)	35 ^a	38 ^a	24	<0.05
Hydrophyllaceae						
	<i>Eucrypta chrysanthemifolia</i>	(A)	0	0	0	ns
	<i>Phacelia minor</i>	(A)	0 ^a	0 ^a	13	<0.001
Onagraceae						
	<i>Camissonia californica</i>	(A)	3 ^a	6 ^a	49	<0.001

TABLE 1. CONTINUED.

	Growth form	Percentage germination			
		Control	120°C 5 min	Charred wood	p
<i>Clarkia epilobioides</i>	(A)	42 ^a	54 ^a	75	<0.001
<i>C. purpurea</i>	(A)	40 ^a	40 ^a	72	<0.05
<i>C. unguiculata</i>	(A)	61	65	68	ns
Papaveraceae					
<i>Dicentra chrysantha</i>	(Hp)	0	0	0	ns
<i>D. ochroleuca</i>	(Hp)	0	0	0	ns
<i>Papaver californicum</i>	(A)	0 ^a	0 ^a	89	<0.001
<i>Romneya coulteri</i>	(S)	0 ^a	0 ^a	40	<0.001
Polemoniaceae					
<i>Gilia australis</i>	(A)	31 ^a	32 ^a	80	<0.001
<i>G. capitata</i>	(A)				
Mature chaparral#		8 ^a	22 ^a	83	<0.001
Burned chaparral#		20 ^a	25 ^a	69	<0.001
Polygonaceae					
<i>Chorizanthe fimbriata</i>	(A)	37	29	45	ns
<i>Pterostegia drymarioides</i>	(A)	68	30	47	<0.01
Ranunculaceae					
<i>Delphinium cardinale</i>	(Hp)	50 ^a	2	40 ^a	<0.001
<i>D. parryi</i>	(Hp)	68 ^a	30	61 ^a	<0.0
Rubiaceae					
<i>Galium angustifolium</i>	(Hp/S)	22	17	43	<0.001
<i>G. parisiense</i>	(A*)	85	89	100	ns
Scrophulariaceae					
<i>Antirrhinum coulterianum</i>	(A)	2 ^a	3 ^a	42	<0.001
<i>A. kelloggii</i>	(A)	39 ^a	45 ^a	63	<0.01
<i>A. nuttallianum</i>	(A)	69	56	58	ns
<i>Collinsia parryi</i>	(A)	24	12	77	<0.001
<i>Cordylanthus filifolius</i>	(A)	57 ^a	27	62 ^a	<0.05
<i>Penstemon centranthifolius</i>	(Hp)	0 ^a	2 ^a	16	<0.001
<i>P. heterophyllus</i>	(Hp)	54	4	74	<0.001
<i>P. spectabilis</i>	(Hp)	1 ^a	3 ^a	61	<0.001
<i>Scrophularia californica</i>	(Hp)	82 ^a	67 ^a	25	<0.001
Solanaceae					
<i>Solanum douglasii</i>	(S)	82 ^a	85 ^a	63	<0.01
Amaryllidaceae					
<i>Allium praecox</i>	(Hp)	18	14	18	ns
<i>Bloomeria crocea</i>	(Hp)	55	46	60	ns
<i>Dichelostemma pulchella</i>	(Hp)	100	1	64	<0.001

TABLE 1. CONTINUED.

	Growth form	Percentage germination			
		Control	120°C 5 min	Charred wood	p
Liliaceae					
<i>Calochortus concolor</i>	(Hp)	84 ^a	66	82 ^a	<0.05
<i>C. splendens</i>	(Hp)	89	9	66	<0.001
<i>Chlorogalum parviflorum</i>	(Hp)	46	15	46	<0.01
Poaceae					
<i>Melica imperfecta</i>	(Hp)	42	51	34	ns
<i>Stipa lepida</i>	(Hp)	77	64	64	ns

cause it stimulates germination of many chaparral herbs (Keeley et al. 1985). Seeds were heated in a forced convection oven prior to sowing. For both treatments and a control, in which seeds were not heated and charred wood was not applied, five replicate petri dishes of 50 seeds each were tested. The experiment was initiated by addition of 8 ml of deionized water to all dishes except charred wood treatments, which received 10 ml because of water absorption.

Seeds of some species require a period of low temperature treatment in order to overcome embryo dormancy. Periods of two weeks to two months are commonly employed (Atwater 1980), with the longer periods being required for species from higher elevations and latitudes. Many chaparral species from southern California do not require stratification (J. Keeley, unpubl. data). In this investigation, stratification requirement was not studied; however, all dishes were maintained at 5°C for three weeks prior to incubation at 23°C for two weeks, under a 12 hour photoperiod at approximately 350 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Germination was scored after the pre-chilling treatment and each week at 23°C. To determine if some species might require a longer cold treatment, this cycle of three weeks cold and two weeks at 23°C was repeated once before ending the experiment.

Treatments, including controls, were compared with 1-way ANOVA on arcsin transformed data and the Student-Newman-Keuls multiple range test.

RESULTS

Fifty-seven herbs were tested for their response to charred wood and heat shock (Table 1). Two-thirds of the 22 herbaceous perennial and suffrutescent species germinated readily under 'control' conditions and showed no enhancement with either treatment. These included all of the monocot species tested. The heat treatment of 120°C for five minutes did not stimulate germination of any of the

herbaceous perennials, but the possibility of seeds being stimulated by other heating treatments cannot be ruled out. Heating, however, tended to reduce germination of many herbaceous perennials. In these species, heating was apparently lethal because many of the seeds had rotted by the end of the experiment. Germination of five herbaceous perennial and suffrutescent species was stimulated significantly by charred wood; this response was particularly striking in *Penstemon spectabilis* and *Romneya coulteri*, but also was observed in *Galium angustifolium*, *Penstemon centranthifolius*, and *P. heterophyllus*.

Germination of 20 of the annual species was enhanced significantly by charred wood (Table 1). Some species, e.g., *Papaver californicum* and *Phacelia minor*, showed a nearly complete dependence on charred wood. For other species, e.g., *Antirrhinum coulterianum*, *Camissonia californica*, *Gilia capitata*, *Lepidium nitidum*, *Rafinesquia californica*, *Silene multinervia*, and *Streptanthus heterophyllus*, the presence of charred wood resulted in nearly an order of magnitude greater germination. In others, such as *Agoseris heterophylla*, *Antirrhinum kelloggii*, *Collinsia parryi*, *Clarkia* spp., *Cryptantha intermedia*, *Gilia australis*, *Gnaphalium californica*, *Malacothrix clevelandii*, and *Stephanomeria virgata*, there was often substantial 'control' germination, but an additional 20–50% germination with charred wood.

Heat treatment stimulated the germination of *Lotus salsuginosus*, but reduced the germination of seven other annuals, including species with charred wood stimulated germination. *Agoseris heterophylla* had polymorphic germination behavior related to achene morphology; non-beaked achenes had significantly greater germination with heat and charred wood treatments in contrast to the beaked achenes.

Several common fire-following species, *Dicentra chrysantha*, *D. ochroleuca*, and *Eucrypta chrysanthemifolia*, failed to germinate, despite having seeds that appeared filled and viable (tetrazolium testing was inconclusive due to the very small or rudimentary embryos characteristic of these species).

Timing of germination was variable and not related clearly to growth form or germination response. For example, 90% of the total germination of *Calochortus splendens*, an herbaceous perennial, had occurred by the end of the three week pre-chilling treatment; this pattern also was observed for *Dichelostemma pulchella* and annuals such as *Gilia capitata*, *Heterotheca grandiflora*, *Pterostegia drymarioides*, and *Rafinesquia californica*. Other herbaceous perennials, e.g., *Allium praecox*, *Bloomeria crocea*, *Chlorogalum parviflorum*, *Penstemon spectabilis* and *Scrophularia californica*, and annuals such as *Silene multinervia* and *Stephanomeria virgata* failed to germinate in the cold, but the vast majority germinated within the first week at 23°C. Some species (*Lotus strigosus* and *Silene gallica*) had more

or less equal germination percentages at each scoring period throughout the 10 weeks. *Delphinium cardinale* was particularly slow to germinate, none germinated until the second cold treatment eight weeks after the beginning of the experiment.

DISCUSSION

Germination behavior of fire-following herbs and suffrutescents can be categorized into species with no apparent dormancy (except perhaps a cold 'stratification' requirement) or ones with varying degrees of dormancy that can be overcome, under natural conditions, only by fire-related stimuli such as heat shock or charred wood.

Species with non-dormant seeds. Chaparral species with non-dormant seeds include all herbaceous perennial monocot species, both bulb-forming geophytes and bunch grasses, and many herbaceous perennial dicots, such as *Delphinium* spp., *Lomatium* spp., *Marah macrocarpus*, *Paeonia californica*, *Perezia microcephala*, and *Scrophularia californica* (Table 1; also Sweeney 1956, Everett 1957, Emery 1964, Keeley et al. 1985). The presence of these species on recently burned sites is the result of resprouting from underground vegetative parts; seedlings are uncommon at this time. Unlike most perennials that colonize burned sites via seedlings, these resprouting herbs flower vigorously during the first growing season after fire. We predict that the timing of seedling establishment is most likely in subsequent years after fire and up until the time the area is dominated by shrubs. These species survive in gaps in the shrub cover or under the canopy as dormant bulbs that occasionally produce depauperate growth, but seldom flower (Stone 1951, Stocking 1966, Christensen and Muller 1975a).

Non-dormant seeds also are characteristic of some annual species found commonly on burned sites. Some of these, such as *Agoseris heterophylla*, *Galium parisiense*, *Heterotheca grandiflora*, *Lactuca serriola*, and *Microseris linearifolia* (Table 1), are relatively weedy and produce diaspores capable of distant dispersal. Their presence on first-year burns can be accounted for by colonization from nearby disturbed areas such as road-cuts or natural disturbances. Many of these annuals have heat sensitive seeds and, thus, it is of interest that several disperse seeds in the fall and winter, after the time of most chaparral wildfires. Some of these species produce polymorphic achenes with different germination responses (e.g., *Agoseris heterophylla*, see Table 1, and *Heterotheca grandiflora*, see Flint and Palmblad 1978) that may promote colonization of burned sites.

Other less weedy, annual species also have non-dormant seeds. *Antirrhinum nuttallianum*, *Clarkia unguiculata*, *Cordylanthus filifolius*, *Madia gracilis*, *Pterostegia drymarioides* (Table 1), and *Festuca megalura* (Keeley et al. 1985) are often abundant in gaps in the mature canopy. The seeds of these species are dispersed during the

summer dry season and do not germinate until the following winter wet season. Their presence on burned sites may be from seeds in the soil that were produced by 'gap' plants the previous season or from seeds under the canopy that, due to allelopathic compounds from the shrub overstory, were dormant prior to the fire.

Species with heat-stimulated germination. *Lotus salsuginosus* was the only species in this study with a significant increase in germination following heat treatment (Table 1). Other studies have reported heat-stimulated germination for annuals such as *Apiastrum angustifolium*, *Brassica nigra*, and *Camissonia hirtella*, as well as for suffrutescents such as *Helianthemum scoparium* and *Lotus scoparius* (McPherson and Muller 1969, Christensen and Muller 1975a, Keeley et al. 1985), and some shrubs such as *Ceanothus* spp. (Quick 1935). These species commonly are described as being 'hard-seeded' due to the heavily sclerified seed coats and thick cuticle that hinders imbibition (Atwater 1980). Heat melts or cracks the cuticle, commonly around the hilum or strophiole, and this is sufficient to allow germination because artificial scarification of the seed coat will produce the same stimulatory effect as heating. High soil temperatures may produce the same stimulus as a heat shock during fire and, thus, germination may be stimulated in gaps in the mature canopy as well as on disturbed sites.

Species with charred wood stimulated germination. Germination stimulated by charred wood is a far more specific means of timing seedling establishment to burned sites than is heat. Not surprisingly, such species are strongly associated with burns; sometimes they appear in abundance the first year after fire and then disappear until the next fire (true 'pyrophyte endemics'). Charred wood stimulated germination is widespread in the Hydrophyllaceae. It was first discovered in *Emmenanthe penduliflora* (Wicklow 1977) and later in many species of *Phacelia* (Keeley et al. 1985) and the shrub *Eriodictyon crassifolium* (Keeley 1987). In terms of environmental cues that they are likely to encounter in the field, these species exhibit a nearly complete dependence upon charred wood. Complete dependence upon charred wood also is found in both annual and perennial species of Papaveraceae (Table 1). Other families with species having a significant level of germination stimulated by charred wood include the Asteraceae, Boraginaceae, Brassicaceae, Caryophyllaceae, Onagraceae, Polemoniaceae, Rubiaceae, and Scrophulariaceae (Table 1). Some of these species, e.g., the annual *Gilia capitata* (Table 1), may persist in gaps during fire-free periods and produce seeds that are polymorphic in their germination response. A fraction of the seeds germinate each year and a larger portion remain dormant until after fire when germination is stimulated by charred wood (see also Grant 1949).

Based on the taxonomic distribution of germination responses

observed here, we suggest that the mechanism behind germination stimulated by charred wood is different than that for germination stimulated by heat. Species in these two groups differ in several respects. Unlike seeds that are stimulated by heat shock, which have a smooth thick cuticle impermeable to water, seeds stimulated by charred wood have highly sculptured, reticulate seed coats that are not cutinized heavily. *Emmenanthe penduliflora*, for example, produces dormant seeds that will imbibe water (Sweeney 1956). Thus, it seems probable that the chemical leached from charred wood (apparently an oligosaccharide, Keeley and Pizzorno 1986) acts on some internal component, and affects gas permeability of membranes or provides a chemical stimulus to embryo development. The former hypothesis is supported by the fact that scarification will produce the same effect as charred wood (Wicklow 1977). The latter hypothesis is supported by the fact that artificial application of gibberellic acid can duplicate the charred wood stimulus. For example, germination of *Penstemon spectabilis* and *Romneya coulteri* increased from 1–61% and from 0–40%, respectively, in the presence of charred wood (Table 1) and Atwater (1980) reported increases from 2–70% for *P. spectabilis* and from 0–42% for *R. coulteri* with the addition of gibberellic acid.

Future research will focus on those fire-following species, e.g., *Eucrypta chrysanthemifolia*, *Dicentra corymbosa*, *D. ochroleuca* (Table 1), and *Phacelia brachyloba* (Keeley et al. 1985), that we have been unable to germinate. All of these species are restricted largely to postfire conditions. Atwater (1980) has found that germination of *D. corymbosa* can be accomplished with the addition of gibberellic acid. In light of the fact that in other species gibberellic acid can simulate the effect of charred wood, it is likely that under natural conditions, germination of these species is also cued by charred wood, but apparently in conjunction with some other unknown factor.

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ANNOUNCEMENT

NEW PUBLICATION

PETERSON, P. M., A flora of the Cottonwood Mountains, Death Valley National Monument, California, *Wasmann J. Biol.* 44:73-126, 1986. [On 60 fam., 252 gen., 543 taxa of vascular plants.]

SOME DEMOGRAPHIC AND ALLOMETRIC CHARACTERISTICS OF *ACACIA SMALLII* (MIMOSACEAE) IN SUCCESSIONAL COMMUNITIES

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ABSTRACT

Diameter distributions of *Acacia smallii* Isley were examined in the South Texas Plains Region in a series of successional communities ranging in age from 15 yr to mature stands >150 yr. In the 15 yr stand, all individuals were in the sapling stage and the size class distribution was non-normal and positively skewed. Mid-successional and older woodland communities had distributions that approached normal curves. Mean live basal area of *A. smallii* increased in stands up to 25–29 yr, and then declined. There was no recruitment of *A. smallii* in stands 19 yr or older. The mean number of stems per plant increased and then decreased in the progression from younger to older stands. Dead stems increased from zero in the 15 yr stand to 66% of the *A. smallii* density in the 33 yr stands. Of the total *A. smallii* basal area, ca. 70% was dead tissue in the 33 yr stands. No individuals of *A. smallii* were present in the mature forest community. Possible cause of this lack of *A. smallii* recruitment was the low light environment caused by canopy closure. Demographic analyses of *A. smallii* diameter distributions suggest it is an early successional species.

Acacia smallii Isley (huisache) is found throughout the southern United States from northern Florida to California (Correll and Johnston 1970). In south Texas, it is reported on approximately 1.1 million ha with more than 20% cover occurring in some places (Smith and Rechenthin 1964). *Acacia smallii* is a heliophyte (Bush and Van Auken 1986a), and is tolerant of low levels of soil nitrogen (Van Auken et al. 1985). *Acacia smallii* has been reported as an early successional species in south Texas (Van Auken and Bush 1985); however, there are no reports of demographic or allometric characteristics of this species.

Studies of demographic characteristics of long-lived woody plants in natural plant populations are scarce (Harper 1977). Whittaker (1975) suggested that early successional species, those that would not remain in a mature forest community, developed normal distributions, whereas the mature forest species had negative exponential distributions. Mohler et al. (1978) proposed idealized frequency distributions of trunk diameters for selected stages in succession. During stand establishment, the frequency distribution is a negatively skewed function. After establishment, but before the start of thinning, the distribution approaches a normal curve; at the start of

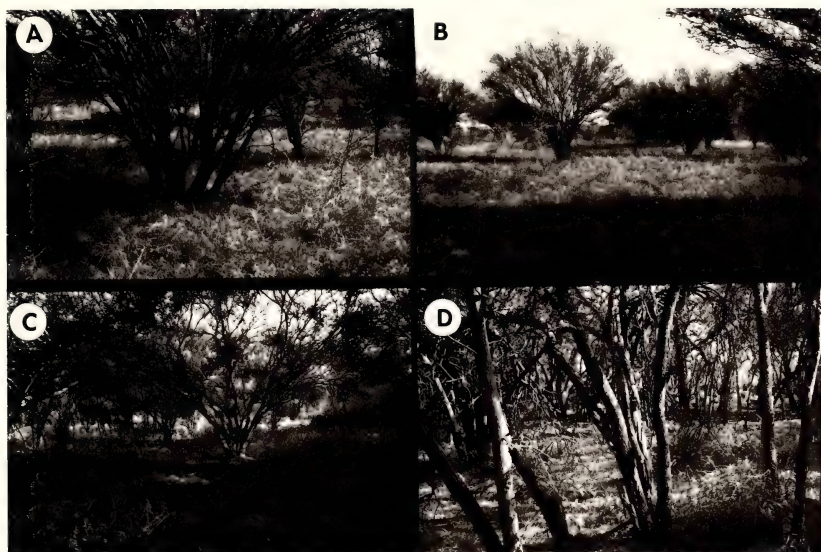
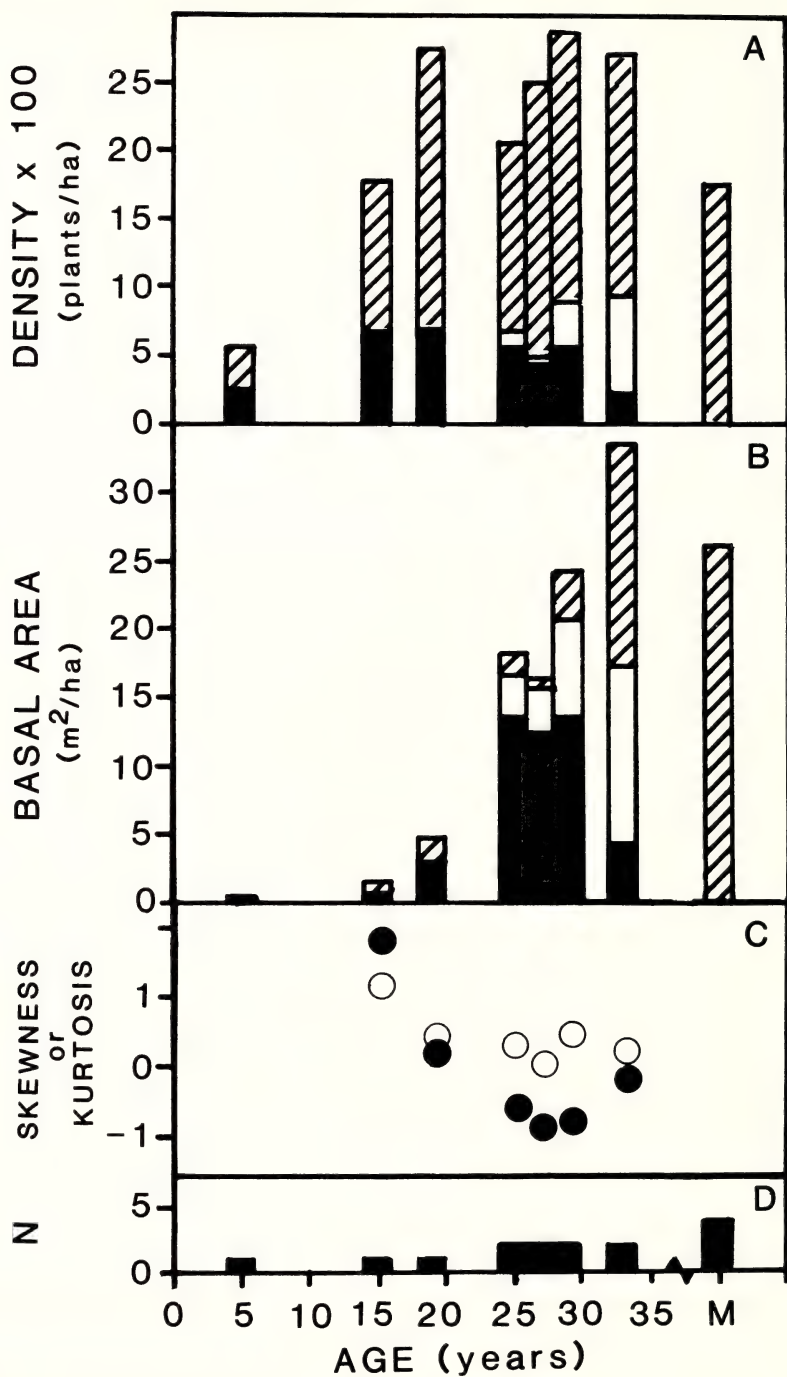


FIG. 1. Habitats of *Acacia smallii* during several stages of secondary succession. A. Multi-stemmed growth form of *A. smallii*. B. Early open savanna or woodland stage with a high grass density in the understory. C. Canopy closure during the late savanna stage. D. Early mature forest stage with most *A. smallii* dead, and the presence of other deciduous species in the overstory.

thinning the distribution is positively skewed. Finally, during late thinning the curve again approaches a normal distribution. Other studies, although less comprehensive, showed that disturbance sequence, site or niche difference, and initial density or spacing were all factors that had a role in determining the demographics of a species (Koyama and Kira 1956, Davidson and Donald 1958, Yoda et al. 1963, Leak 1975, Crisp and Lange 1976, Crisp 1978, Harcombe and Marks 1978, Ross et al. 1982, Knowles and Grant 1983, West and Borough 1983).

In addition to changes in the demographics of a plant population, increased competition causes alterations in the morphology of individual plants (Harper 1977). Morphological changes occur in whole plants, for example, as shown in the annual diameter growth of *Picea sitchensis* (Bong.) Carr. at various spacings (Jack 1971). Additional changes in whole plant morphology were demonstrated in *Pseudotsuga menziesii* (Mirb.) Franco, which showed a larger number of suppressed individuals at higher densities (Curtis and Reukema 1970). Jack (1971) demonstrated a reduction in the number of branches in *Picea sitchensis* grown at high densities.

The purposes of this study were to examine some demographics of population development and decline of *Acacia smallii*, and to



examine some allometric changes of this species associated with temporal change.

METHODS

This study was conducted in the northern portion of the South Texas Plains Region of Texas (Gould 1969). Fifteen communities in various stages of secondary succession were selected for detailed analyses. The sites were located on flood plain terraces of the San Antonio River, which potentially support riparian woodland or forest communities (for locations see Van Auken 1982, Bush and Van Auken 1984). Climate of the upper San Antonio River area is dry subhumid (Thornthwaite 1948). This area receives approximately 71 cm/yr rainfall, with a mean annual temperature of 15.5°C (Carr 1967, Arbingast et al. 1976). Soils are deep loams (240–310 cm), that usually are well drained, calcareous, and friable (Taylor et al. 1966, Taylor 1977).

Candidate stands were examined during a series of field surveys. Stands also were located on aerial photographs and soil survey maps, and local residents were interviewed concerning past history of the sites. Selection was based on stand area, lack of additional disturbance other than light grazing in the mature communities, uniformity of physical features, and vegetation. Selected stands depicted various stages in a chronological sequence from open fields to mature forests.

The stands selected for study were 1–5 ha in size, and the area sampled in each stand ranged from 0.1–0.5 ha. Most of the stands were cleared in the 1950's. The mature stands were estimated to be in excess of 150 yr, as based on tree ring analyses.

Stands were sampled using belt transects, with 5 m × 5 m quadrats (Greig-Smith 1983). Density and basal area for all species except *A. smallii* were pooled. All stems greater than 1.0 cm in diameter at breast height were used to construct diameter distribution plots.

Demographic characteristics for the various stands were analyzed by size class (diameter). The width of the size classes in each stand was determined by dividing the range of diameters into 12 equal size classes (Mohler et al. 1978). Statistical tests included Chi-square analysis to test for normal distributions and a "t" statistic to test for skewness (g_1 , asymmetry) and kurtosis (g_2 , peakedness) (Sokal

FIG. 2. Live (■) and dead (□) standing stem density (A) and basal area (B) for *Acacia smallii* and all other woody species combined (▣) for a series of successional stands. Asymmetry (skewness = ○) and peakedness (kurtosis = ●) of the *A. smallii* populations also are presented (C) with the number (N) of stands sampled (D). M = mature stands greater than 150 yr old.

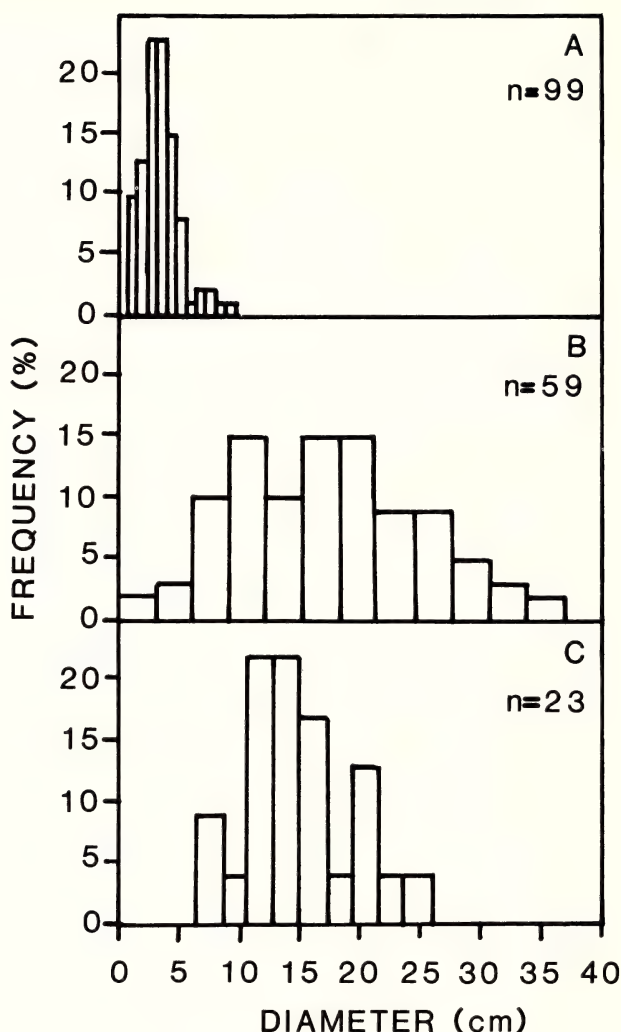


FIG. 3. Frequency distribution of live stems of *Acacia smallii* in secondary succession including a 15 yr stand (A), a 27 yr stand (B), and a 33 yr stand (C). n = the total number of plants measured in each stand, the distributions are not normal (Chi-squared, $p \leq 0.05$).

and Rohlf 1981). An example of a 15, 27, and 33 yr stand is presented. Several morphological characteristics of *A. smallii* were examined including the number of stems per plant and the number and percent of dead stems per plant for each stand.

For determination of stand age, 52 plants of *A. smallii* (of various sizes and from various stands) were cored using the increment coring

technique (Fritts 1976). Regression analysis (Steel and Torrie 1980) was performed between tree diameter and tree age using all 52 samples ($r = 0.88$, $p \leq 0.001$). Next, the diameters of the five largest trees in each stand were used to estimate the stand age. Stand age was determined by adding 5 yr to the mean tree age (from regression) to account for seed recruitment and an additional 3 yr to account for growth from ground level to breast height (measured differences).

RESULTS

Some typical flood plain terrace habitats that include *A. smallii* are shown in Fig. 1. Secondary succession begins with a community disturbance. Within 5 yr, *A. smallii* and other woody species colonize the area (Fig. 2A). *Acacia smallii* increased in density and basal area for the next 25 yr and dominated the stands (Fig. 2A,B). Dead *A. smallii* first appeared in 25 yr stands. Of the total standing basal area in 25 yr stands, ca. 16% was dead *A. smallii*. This value increased to ca. 39% of the total standing basal area in the 33 yr stand. In the 33 yr stand, 74% of the *A. smallii* basal area was dead tissue. *Acacia smallii* density followed a similar trend. Species composition shifted and stands greater than 30 yr had a high density and basal area of *Celtis laevigata* Willd. *Acacia smallii* was not present in the mature stands, which were dominated by *C. laevigata*, *Carya illinoensis* (Wang.) K. Koch. and *Ulmus crassifolia* Nutt. (see Bush and Van Auken 1984, Van Auken and Bush 1985).

None of the stands examined had statistically normal distributions for *A. smallii* (Chi-square analyses $p \leq 0.05$). Skewness decreased from the highest value (1.08) in the 15 yr stand and approached zero in older stands (Fig. 2C). Kurtosis also was highest (1.90) in the 15 yr stand, but decreased to ca. -1 in the 25–29 yr stands and approached zero in the oldest stands.

The diameter distribution for the 15 yr stand was a significant, positively skewed function ($g_1 = 1.08$; $t = 4.41$, $p < 0.001$) (Fig. 3A). The distribution was also leptokurtotic (peaked) ($g_2 = 1.90$; $t = 3.88$, $p < 0.001$). The largest individual in this stand was ca. 10 cm in diameter. The 27 yr stand was not skewed, but was platykurtotic (flattened); however, neither value was statistically significant (Fig. 3B). The largest individual was ca. 37 cm in diameter or 3.7 times larger than the largest tree in the 15 yr stand. In the 33 yr stand, the distribution was slightly, positively skewed and was platykurtotic (Fig. 3C). No individuals were found in the smallest size classes. The largest individual was 26 cm in diameter. No *A. smallii* plants were found in the mature stands (> 150 yr).

The number of stems per plant (both live and dead) for *A. smallii* was time dependent (Fig. 4). In the 15 yr stand, number of stems per plant ranged from 1–17 with no dead stems (Fig. 4A). In the 27

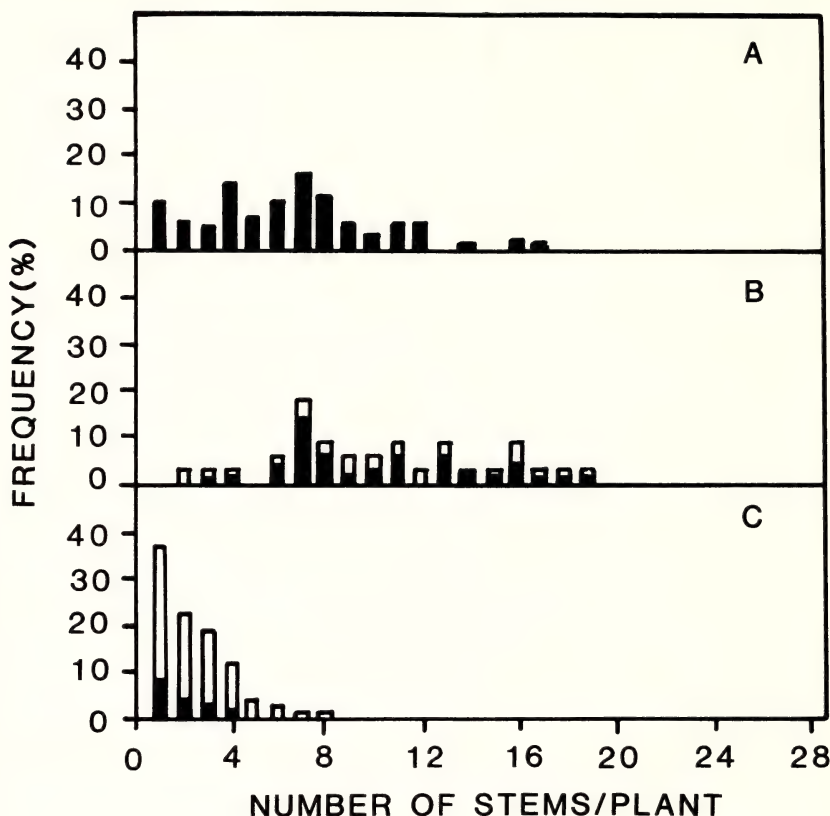


FIG. 4. Frequency distribution of number of stems/plant in a 15 yr stand (A), a 27 yr stand (B), and a 33 yr stand (C). ■ = live stems; □ = dead stems.

yr stand, number of stems per plant ranged from 2–18. There were no single stemmed plants and those standing with 2 stems were dead. In general, almost all other plants had 50% dead stems (Fig. 4B). In the 33 yr stand, number of stems was reduced to 1–8 per plant, more than 50% of the stems per plant were dead, and many of the larger trees were dead (Fig. 4C).

DISCUSSION

In many areas of southern Texas, *Acacia smallii* is a pioneer woody species that colonizes abandoned farmland or rangeland. Although it increases in density and basal area, community dominance of *A. smallii* only lasts approximately 30 yr, at which time it is replaced by mature community species (Van Auken and Bush 1985). Demographic characteristics examined showed the fate of *A. smallii* in

older stands. Density decreased and basal area increased, as has been shown for other early successional forest species (e.g., Spurr and Barnes 1973). Furthermore, a self-pruning of stems occurred; thus, the tendency of growth form was toward single stemmed trees in older communities. Finally, with overtopping by *Celtis laevigata* and subsequent additional shading, the remaining trees died.

Acacia smallii seems to follow the pattern of frequency distribution that was proposed by Mohler et al. (1978) for *Prunus pennsylvanica* L. In the present study, the 15 yr stand was well beyond their "establishment" and "transition" stages, but was similar to their "start of thinning" stage, which is a positively skewed function. Phytosociological data showed an increase in the basal area of *A. smallii* from the 15–27 yr stands, but a 46% decrease in density, which supports the start of thinning hypothesis. Although none of the frequency distributions in the present study were normal, the distribution in the late successional community did approach a normal curve similar to the "late thinning" stage.

The differences between the present study and the frequency distributions of single species proposed by Mohler et al. (1978) are probably due to several factors. In addition to intraspecific competition that causes thinning in plant populations, interspecific competition was probably also playing a critical role in shaping the frequency distribution of *A. smallii*. In the early stand, thinning was most likely through the death of the smallest individuals; however, in the mid- and late stands, death occurred to parts of whole plants before the individuals died. Whereas in the early stands none of the individuals had dead stems, the mid- and late stands showed increased death to stems of individuals. In addition, in the mid- and late stands, there was no recruitment of *A. smallii*.

Whittaker (1975) suggested that colonizing species would develop bell-shaped frequency distributions, whereas mature community species would have negative exponential distributions. This is probably an oversimplification, and dependent on episodic seedling establishment. Furthermore, his data suggested that, as the population of a colonizer ages, the distribution remained normal, but frequency of individuals in each size or age class would be reduced by deaths.

Changes in the available resources in a temporal sequence greatly affect the competitive ability of the species involved and, therefore, affect the frequency distributions. *Acacia smallii* is a heliophyte and tolerates low levels of soil nitrogen (Van Auken et al. 1985, Bush and Van Auken 1986a). Consequently, early in succession, *A. smallii* is a better competitor than late community species, which require higher levels of soil nitrogen (Van Auken et al. 1985, Bush and Van Auken 1986a). In early stands, therefore, intraspecific competition is probably more intense for *A. smallii* than interspecific competition; hence, smaller individuals often die. In older stands,

light becomes limiting and soil nitrogen levels favor the late community species (Bush and Van Auken 1986a,b). These conditions apparently do not allow recruitment of *A. smallii* (Van Auken and Bush 1985), whereas interspecific competition affects the larger individuals through the death of stems and, finally, the death of the trees. In the mature forest, *A. smallii* disappears and species such as *Celtis laevigata* dominate because they are better competitors in the canopy shade.

ACKNOWLEDGMENTS

This study was supported in part by the U.S. Department of the Interior, National Park Service. We especially thank Ms. M. Bush Thurber and Mr. J. Cisneros of the San Antonio Missions National Historical Park for their encouragement. We are grateful to Mr. and Mrs. W. Southern for access to their land along the San Antonio River and to Mr. D. Riskind of the Texas Parks and Wildlife Department for access to undeveloped parkland in the same area. We also thank Dr. D. C. Randall and an anonymous reviewer for many helpful comments and corrections.

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ANNOUNCEMENT

NEW PUBLICATION

GRAYSON, A. J., *Birds of the Pacific Slope*, The Arion Press, 460 Bryant St., San Francisco, CA 94107, 1986, \$45.00. [Includes a portfolio of 165 bird portraits (full-scale facsimiles), reproducing all surviving paintings (California and Mexico from 1853-1869) from the Bancroft Library (UC); a book with preface by S. D. Ripley; and a biography of the artist and naturalist by Lois C. Stone (long-time member of the California Botanical Society), with bird biographies and field notes by Grayson and current ornithological descriptions for each plate. Excellent plant and landscape paintings are associated with the portraits. This work is considered by some authorities to be the most important contribution to American Ornithology (i.e., illustrations and biographies) next to the work of Audubon.]

MYCORRHIZAE ASSOCIATED WITH AN INVASION OF
ERECTHITES GLOMERATA (ASTERACEAE) ON
SAN MIGUEL ISLAND, CALIFORNIA

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ABSTRACT

Erechtites glomerata (Australian fireweed) is a perennial alien species that recently has invaded San Miguel Island, an island off the coast of southern California. It is presently advancing into a grassland dominated by *Distichlis spicata* and with scattered shrubs. As is typical of many weedy species, *E. glomerata* is facultatively mycotrophic on the island. Levels of colonization by vesicular-arbuscular mycorrhizal (VAM) fungi ranged from 0–30% of the root system. Nine species of VAM fungi were recovered from its root zone.

Australian fireweed, *Erechtites glomerata* (Poir.) DC. (Asteraceae), is a native of Australia and New Zealand that has been advancing slowly into the southern California region. It is a perennial that grows to 2 m in height. The common name "fireweed" comes from Australia and refers to the invasive nature of the plant in burn areas; however, it also can easily invade cleared or otherwise disturbed sites (Taylor 1964). On San Miguel Island, Santa Barbara Co., California, it has invaded and spread through a stable native grassland community (Fig. 1).

Vesicular-arbuscular mycorrhizae (VAM) are intimate, mutualistic associations formed between certain Zygomycetous fungi and plant roots. The fungi apparently are obligate symbionts, obtaining the bulk of their nutritional requirements from the "host" plant (Harley and Smith 1983). The fungi occupy the cortical cells of roots and produce hyphae that grow a few cm into the surrounding soil where they absorb phosphate that is beyond the root's depletion zone. Numerous studies (e.g., Nelsen and Safir 1982, Harley and Smith 1983, Fitter 1985) have shown that VAM ameliorate the effects of water stress and reduced availability of phosphorus in the soil. Growth improvements of up to 1100% have been achieved when plants growing in phosphorus-deficient soils were inoculated with VAM fungi (Mosse 1972).

VAM associations are extremely common, occurring in 95% of



FIG. 1. *Erechites glomerata* in a grassland community on San Miguel Island, California.

all plant families (Trappe in press). Although present in most soils, VAM fungi sometimes are absent from certain sites. The presence or absence of VAM fungi in soil can influence the ability of different plant species to establish in an area (Janos 1981, Miller 1979, Reeves et al. 1979). Plant species that require association with VAM fungi to complete their life cycle (=obligate mycotrophs) are unable to successfully invade and persist in sites that lack propagules of VAM fungi. Such VAM-free sites, therefore, are preferentially colonized by plant species that do not have an absolute requirement for VAM. These plant species are classified as non-mycotrophs or facultative mycotrophs, depending upon their ability to form VAM when the appropriate fungi are present. Because they grow well whether or not VAM fungi are present in the soil, facultative mycotrophs include many of the most troublesome weedy species (Trappe in press).

We examined plants of *E. glomerata* to determine their mycorrhizal status and to help explain their ability to be so invasive on San Miguel Island, a natural area managed by the National Park Service that functions under policy that calls for the removal of all such invasive, noxious weeds.

STUDY AREA

San Miguel is a 4000 ha island off the coast of southern California. It is the westernmost of the northern Channel Islands, occurring

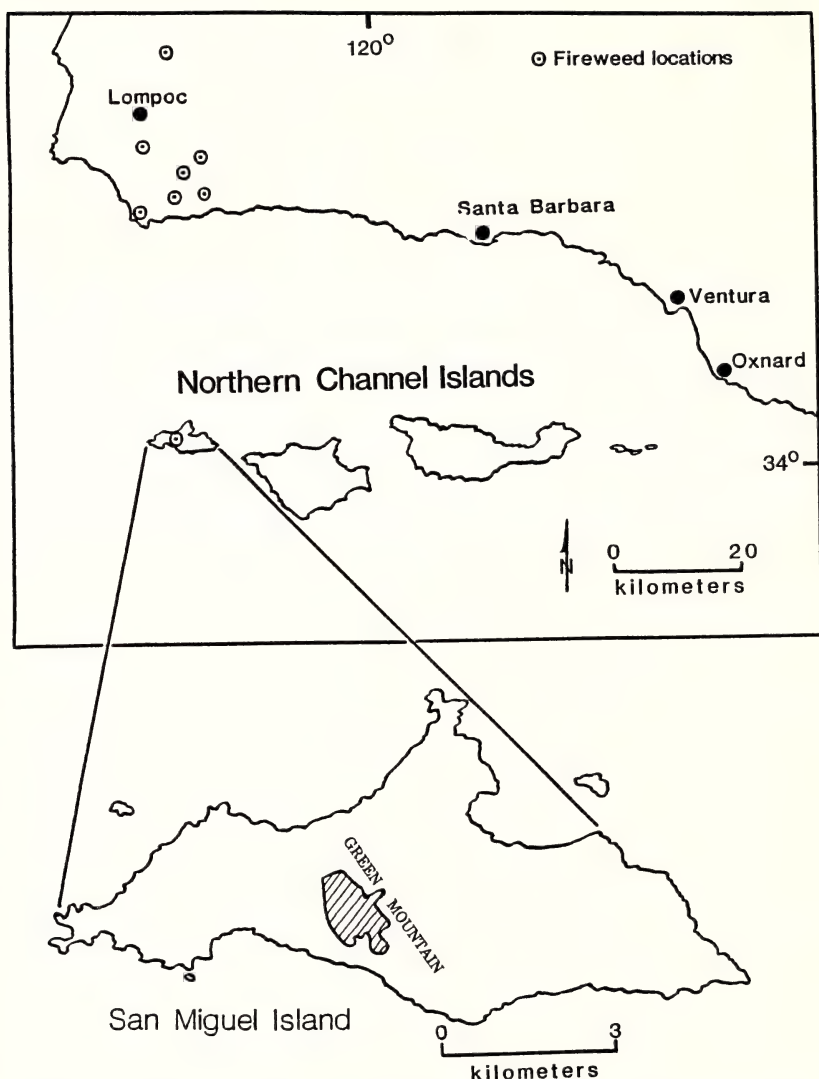


FIG. 2. Location of San Miguel Island in the southern California Bight area, showing the distribution (shaded area) of *Erechites glomerata* (Australasian fireweed).

about 45 km south of Point Conception and 100 km west-southwest of Ventura (Fig. 2). Bedrock on the island is composed primarily of Cretaceous and early to mid-Tertiary conglomerates, sandstones, siltstones, shales, and volcanics. Structurally, the island represents the north flank of a folded and faulted anticline, whose axis trends northwest-southeast (Johnson 1979, Weaver et al. 1969). Much of

the island is covered with sand, both stabilized and unstabilized. In the area that is the subject of this report, the soils are of the vertisol type with a high level of expandable clay and shrink-swell characteristics (Johnson 1979).

The specific weather/climate characteristics of the island are relatively undefined due to a lack of adequate data. The island lies in the dry-summer, subtropical climate, commonly called Mediterranean (Trewartha 1954). Rainfall is in the range of 330–355 mm per year and the mean annual temperature is 13.7°C with an annual range of 3°C. The two most characteristic features of the weather are wind and fog. The wind is almost constant and comes principally out of the northwest. The winds commonly blow 30–40 km/hr with gusts up to 60 km/hr; strong northwest flows during the period of winter storms, bring winds of 70–80 km/hr. Morning fog is common throughout the year, but it is most constant during the summer months (Dunkle 1950, Weissman and Rentz 1977, NPS files).

The most important plant community on the island is grassland. There are two types: those dominated by introduced *Avena* (*A. fatua* L. and *A. barbata* Brot.) and *Bromus* (*B. mollis* L., *B. rubens* L. and *B. diandrus* Roth) and those dominated by the native *Distichlis spicata* (L.) Greene. Other community types include scrub dominated by *Haplopappus venetus* (HBK.) Blake, and coastal sage scrub, coastal bluff, coastal dunes, and a small coastal salt marsh (Hochberg et al. 1979).

METHODS

The island was surveyed carefully in January 1985, and the total areal extent of the *Erechtites* population was mapped. One hundred quadrats (1 × 1 m) were placed randomly throughout the invasion area to assess the density of the population and to determine the species composition of the grassland community.

Root and soil samples were collected in July and November 1985, to determine the status of mycorrhizae. Roots of six specimens of *E. glomerata* were fixed in the field in formalin : acetic acid : ethanol : water (2:1:5:7, v/v/v/v). In the laboratory, roots were cleared and stained using a modification of the method of Phillips and Hayman (1970). The fixed roots were cleared by autoclaving for 3 minutes in 10% KOH. Cleared roots were rinsed in a dilute HCl solution, and mycorrhizae were stained by autoclaving the roots for 3 minutes in 0.05% trypan blue in lactic acid : glycerol : water (1:2:1, v/v/v). Roots were destained by autoclaving for 3 minutes in the above solution without trypan blue.

The extent of colonization of roots by VAM fungi was determined by estimating the percent (to nearest 10%) of the length of the absorbing root system that contained arbuscules, vesicles, hyphal coils, or internal hyphae of VAM fungi.

To determine the species of VAM fungi associated with the plants,

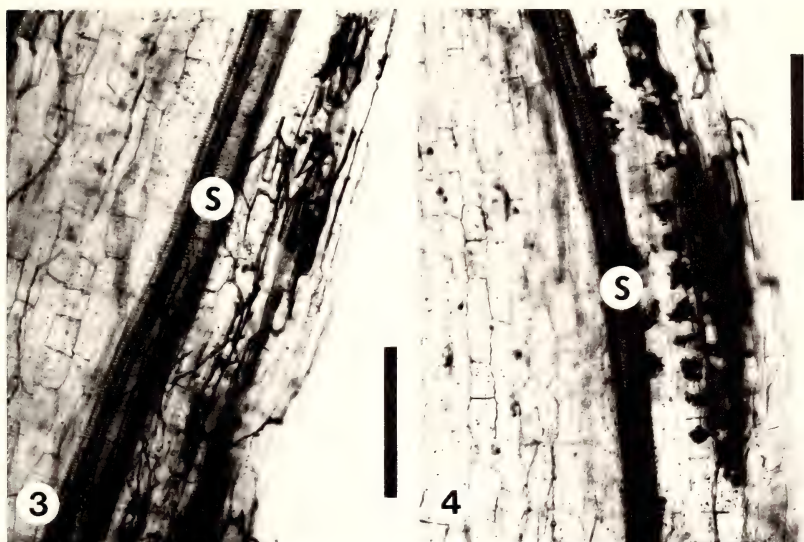
TABLE 1. COMPOSITION OF THE GRASSLAND COMMUNITY INTO WHICH *Erechtites glomerata* IS INVADING ON SAN MIGUEL ISLAND. Presence (%) was derived by dividing the number of plots in which a species was found by the total number of plots sampled. * = species that are considered alien to the San Miguel Island flora.

Species	Presence (%)
<i>Distichlis spicata</i> (L.) Greene	94
* <i>Medicago polymorpha</i> L.	58
<i>Amsinckia intermedia</i> F. & M.	32
* <i>Stellaria media</i> (L.) Vill.	18
<i>Malacothrix incana</i> (Nutt.) T. & G.	16
* <i>Galium aparine</i> L.	14
* <i>Sonchus oleraceus</i> L.	14
<i>Calystegia macrostegia</i> (Greene) Brummitt	10
<i>Lupinus succulentus</i> Dougl. ex Koch.	8
<i>Dichelostemma pulchellum</i> Heller	6
<i>Eschscholzia californica</i> Cham.	4
<i>Atriplex californica</i> Moq. in DC.	4
* <i>Atriplex semibaccata</i> R. Br.	4
* <i>Daucus pusillus</i> Michx.	4
<i>Astragalus curtipes</i> Gray	2
<i>Chenopodium californicum</i> (Wats.) Wats.	2
* <i>Erodium moschatum</i> (L.) L'Her.	2

soil samples (ca. 500 cc) were collected from the root zones of two plants. A 75 cc subsample composed of 20–30 smaller subsamples withdrawn from the 500 cc sample was processed to recover spores. Spores were extracted from the soil by a water-sucrose centrifugation technique (Walker et al. 1982). Following centrifugation, spores were collected on a 5.5 cm filter paper (Whatman no. 1) in a Buchner funnel. The filter paper was examined at 30× with a dissecting microscope, and spores were removed, mounted in a polyvinyl alcohol mountant (Koske and Tessier 1983) and identified with the aid of a compound microscope at 400–1000×. Identifications were confirmed by comparison with type or authenticated specimens and by consultation with VAM taxonomists. Voucher specimens have been deposited in the mycological herbarium at the University of Rhode Island. Nomenclature of higher plants follows Munz (1968) except for *Erechtites glomerata*, which follows Barkley (1981). Nomenclature for fungi follows original authors that are given in Table 2.

RESULTS

The grassland that *Erechtites glomerata* is invading on San Miguel Island (Table 1) is dominated by *Distichlis spicata* with scattered patches of forbs, particularly *Amsinckia intermedia*, *Eschscholzia californica*, *Calystegia macrostegia*, *Chenopodium californicum*, *Sanicula arguta*, and *Dichelostemma pulchellum*. Scattered shrubs,



FIGS. 3, 4. VAM fungi in roots of *Erechites glomerata*. Stele is indicated ("S"), scale bar is 50 μ m. 3. Hyphae and hyphal coils. 4. Arbuscules and hyphae in cortical cells.

including *Baccharis pilularis* subsp. *consanguinea* and *Solanum douglasii*, also are present.

The flora of San Miguel Island was surveyed in 1978–79 (Hochberg et al. 1979), and no plants of Australasian fireweed were found. Plants of *E. glomerata* were first observed in May 1984, and the species was well established at that time (Junak pers. comm.). In January 1985, we determined that it covered an area of approximately 70 ha to the west of Green Mountain. Densities of stems within the population showed a pattern of spread from north to south in response to the prevailing winds. Density at the point of origin was 8800/ha. This decreased to 2100/ha and finally 500/ha with increasing distance southward.

TABLE 2. SPECIES OF VESICULAR-ARBUSCULAR MYCORRHIZAL (VAM) FUNGI ISOLATED FROM THE ROOT ZONE OF *Erechites glomerata*.

<i>Acaulospora laevis</i> Gerd. & Trappe (Gerdemann and Trappe 1974)
<i>Entrophospora infrequens</i> Ames & Schneider (Ames and Schneider 1979)
<i>Gigaspora calospora</i> (Nicol. & Gerd.) Gerd. & Trappe (Gerdemann and Trappe 1974)
<i>Glomus aggregatum</i> Schenck & Smith (Schenck and Smith 1982)
<i>Gl. intraradices</i> Schenck & Smith (Schenck and Smith 1982)
<i>Gl. pansihalos</i> Berch & Koske (Berch and Koske 1986)
<i>Gl. scintillans</i> Rose & Trappe (Rose and Trappe 1980)
<i>Gl.</i> 598 (spores yellow-brown to red-brown, 70–140 μ m diam., thick-walled)
<i>Gl.</i> 2163 (spores pale yellow, 60–120 μ m diam., thin-walled)

Five of the six plants of Australasian fireweed sampled possessed vesicular-arbuscular mycorrhizae (Figs. 3, 4), with levels of VAM colonization ranging up to 30% (\bar{x} = 14%). Nine species of VAM fungi were isolated from the root zone of *E. glomerata* (Table 2). Species that produced the most numerous spores in association with this host were *Glomus pansihalos* and *Gigaspora calospora*. Two of the species, *Glomus* 598 and *Gl.* 2163, could not be assigned to existing taxa and apparently are undescribed new species.

DISCUSSION

Erechtites glomerata is an aggressive alien that newly inhabits San Miguel Island. Introduction apparently resulted from seeds being carried across the Santa Barbara Channel from the mainland (Fig. 2). At this time, it is found nowhere else on the Channel Islands. Although in its native Australia it is most common in burned or disturbed areas, on San Miguel Island this fireweed is invading an established native grassland. Its spread has been rapid and effective with fireweed becoming a major component of the grassland community.

We have found eight of the nine species of VAM fungi recovered in the present study occurring in association with native plant species on San Miguel Island, a typical situation because VAM fungi usually have wide host ranges (Harley and Smith 1983). *Glomus scintillans*, the one species that has not been found thus far in the root zones of other plants on the island, was described originally from a shrub desert site in eastern Oregon (Rose and Trappe 1980), where it was associated with shrubs that harbor nitrogen-fixing actinomycetes in their roots.

Of the six other species that have been described previously, four have been found in the southwestern U.S.: *Entrophospora infrequens* in mainland Ventura Co., California (Ames and Schneider 1979, Nemec et al. 1981); *Acaulospora laevis*, *Entrophospora infrequens*, *Gigaspora calospora*, and *Glomus intraradices* from the Sonoran Desert in Arizona (Bloss 1986); and *Glomus intraradices* from Anza Borrego State Park in southern California (Bethlenfalvay et al. 1984). The other two species (*Glomus aggregatum* and *Glomus pansihalos*) have been found in the Great Lakes Region and on the east coast of the United States (Koske 1987, Koske and Tews in press, P. Olexia, pers. comm.).

Erechtites glomerata appears to be a facultative mycotroph that fits within the pattern of tropical weedy species in which those plants that produced light seeds were shown to be the least dependent upon mycorrhizae (Janos 1980). This characteristic explains in part why *E. glomerata* is such a successful invader, and should be considered in any management strategy that the National Park Service might develop for its control or removal.

ACKNOWLEDGMENTS

We thank Steve Junak for his assistance in determining the location of *E. glomerata*, for help in the field, and in reviewing this manuscript, and Chris Walker and Joe Morton for their assistance in identifying the fungi. Field assistance was provided by Ronie Clark and Frank Ugolini. The study was supported by the National Park Service Science Program.

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(Received 5 May 1986; revision accepted 9 Mar 1987.)

NOTEWORTHY COLLECTIONS

BRITISH COLUMBIA

SALIX TWEEDYI (Bebb) C. R. Ball (SALICACEAE).—Bolean Lake, northeast of Falkland. 50°32'N, 119°30'W, 1440 m, in a *Salix*, *Carex* swamp at s. end of lake in front of resort, associated with *S. barclayi*, 25 Jul 1986, T. C. Brayshaw 86-23, -24, -26, -27, -28, -29, -30 (CAN, V).

Previous knowledge. This species was first collected in Canada at this locality in 1941 by C. L. Hitchcock and J. S. Martin. Their collection number 7524 was distributed as *S. barclayi* Anderss. In 1962, A. Cronquist recognized that a duplicate at NY was actually *S. tweedyi*. This specimen evidently was the basis for the inclusion of BC in the distribution of the species in Hitchcock et al. (*Vascular Plants of the Pacific Northwest* 2:69, 1964). Specimens of 7524 in RM and WTU also are *S. tweedyi*, but the specimen in A was correctly named *S. barclayi*.

Significance. These collections confirm the occurrence of *S. tweedyi* in Canada at a locality about 200 km n. of its nearest locality in Washington (Okanogan Co., Tiffany Mt.). This species is rare in BC.—GEORGE W. ARGUS, National Herbarium, Museum of Natural Sciences, Ottawa, ON K1A 0M8 and T. C. BRAYSHAW, British Columbia Provincial Museum, Victoria, BC V8V 1X4, Canada.

NEW MEXICO

SALIX GEYERIANA Anderss. (SALICACEAE).—Catron Co., Mogollon Mountains, Gilita Cr. at confluence of Indian Cr., ca. 31 km e. of Mogollon, 33°24'N, 108°34'W, 8000

ft, dominant in *Salix* thicket along creek, 27 Jun 1986, *G. W. and J. N. Argus* 12258, 12263 (CAN). Luna, on US 180, 3.4 km w. of town at crossing of San Francisco River, 33°50'N, 109°01'W, 7500 ft, *Populus angustifolia* thicket on creek margin, 2 Jul 1986, *G. W. and J. N. Argus* 12394 (CAN). Luna, on US 180, 2 km w. of town, 33°50'N, 108°59'W, 7100 ft, *Salix irrorata* dominated thicket in wet meadow, 2 Jul 1986, *G. W. and J. N. Argus* 12398 (CAN).

Previous knowledge. Occurs in the Rocky Mountains from southern British Columbia to Colorado and in California with disjunct localities in western Nebraska and the White Mountains of Arizona.

Significance. New to the flora of New Mexico. This occurrence in the Mogollon Mts. parallels the disjunction in the White Mts. of Arizona.—GEORGE W. ARGUS, National Herbarium, Museum of Natural Sciences, Ottawa, ON K1A 0M8, Canada.

FESTUCA MINUTIFLORA Rydb. (POACEAE).—Rio Arriba Co., Pecos Wilderness Area, North Truchas Peak, w. slope of mountain, 35°59'N, 105°37'W, 12,000 ft, alpine vegetation on talus slope, 4 Jul 1986, *G. W. and J. N. Argus* 12404 (CAN) (identified by Susan Aiken).

Previous knowledge. Scattered throughout the w. states (AZ, CA, CO, OR, UT, WY) at elevations between 3000–4000 m. It is relatively common in Colorado, but poorly known elsewhere (Frederiksen, Bot. Notiser 132:315–318, 1979).

Significance. New to the flora of New Mexico.—GEORGE W. ARGUS and SUSAN G. AIKEN, National Herbarium, Museum of Natural Sciences, Ottawa, ON K1A 0M8, Canada.

REVIEWS

Xántus, The Letters of John Xántus to Spencer Fullerton Baird from San Francisco and Cabo San Lucas, 1854–1861. Introduction, Notes and Illustrations by ANN H. ZWINGER. 442 pp. Dawson's Book Shop, Los Angeles. 1986. \$69.00.

Any biologist concerned with natural history in Baja California, Mexico, is familiar with the specific epithets *xanti* or *xantusii*. John Xántus de Vesey sailed from San Francisco in March 1859 during our spring and arrived to Cabo San Lucas in early April, at the height of the dry season there. It is small wonder that in his first letter he said, "There is not a drop of water for a distance of 28 miles (San Jose) only Mr. Ritchie has a well, of very indifferent brackish water, and there is not a tree for many miles, if we except the Cactuses, of which there is infinite variety. . . ." Xántus installed a tidal gauge, which was the reason for the U.S. Coastal Survey having sent him to the tip of Baja California, and began to collect natural history specimens for the Smithsonian Institution. This was a field of endeavor in which he excelled and one that he much preferred to that of recording tidal data.

These letters to Mr. Baird, the newly appointed Assistant Secretary to Smithsonian Institution in Washington, DC, show the difficulties under which Xántus carried on his work. He had to take all scientific equipment with him; mail sometimes took six months or more to reach him. Shipment of his scientific specimens depended upon unscheduled arrival of whalers or ships that were bound for San Francisco or eastern seaboard ports. His letters contain meticulous reports on the contents of each shipment

and of collecting conditions, but the most that they say of the people in the little pueblo of Cabo San Lucas is that boys sometimes brought him specimens. That there were people there is brought out by Professor Emeritus Herbert Mason's story about his brief time ashore at Cabo San Lucas in 1925, when the California Academy of Sciences' expedition stopped there during its return trip from the Revillagigedo Islands. An elderly *paisano* who was watching while specimens were being put into a plant press remarked, "Mi papá tenía uno de estos." "Who was your papa?" "Xántus." The man couldn't have been much more than a baby at the time Xántus went from Cabo San Lucas on very short notice; so Xántus must have left more than collecting equipment behind! In 1940 when Steinbeck and Ricketts touched at Cabo San Lucas (cf. Zwinger footnote, p. 324) the manager of the cannery, pointing to three little Indian children said, "Those are Xanthuses great-grandchildren," and "in the town there is a large family of Xanthuses."

The paucity of detail about life of the people is undoubtedly due to the fact that Xántus' letters to Baird were business letters detailing progress of his work and difficulties encountered. In one letter, however, Xántus includes a list of 14 donors of scientific material. Typical of these is item No. 8, "Donnas Juana & Pachita Dodero, 10 nests, with 34 eggs, & several bottles of insects." In contrast to his usual letters is that of 28 December 1860 in which he says, "The Christmas day I spent in San Jose, amongst bullfights, cockfights, & dancing. There was a great concourse [sic] of people. . . . The whole fiesta [sic] went off however very decently & with great order, more so than a 4th of July in a small American village." His letters to his mother in Hungary were replete with exciting accounts of his expeditions and adventures—many of them undoubtedly more fancy than fact.

Ann Zwinger's introductory chapter (36 pp.) provides a biographical background for Xántus and brings out the important role that Spencer Fullerton Baird played in building up natural history collections at Smithsonian. Zwinger's copious footnotes to the letters contribute important historical data as to the identity of people mentioned in the letters as well as clarification of some of the scientific names that Xántus cited in his lists. These footnotes not only add to the interest of the book, but also make it historically valuable. An extensive bibliography of the works cited and an unusually full index add to the usefulness of this volume. Because of her long interest in and association with the Cape Region of Baja California, as evidenced by her book *A Desert Country Near the Sea*, Ann Zwinger is especially well-fitted to present this treatment of Xántus.

The Castle Press is to be complimented on a good job of printing the difficult material. This is a worthy addition to Glen Dawson's series on Baja California.—ANNETTA CARTER, Dept. of Botany, Univ. of California, Berkeley 94720.

Flora Fanerogamica del Valle de Mexico. Volumen II. Dicotyledonae (Euphorbiaceae—Compositae). Edited by JERZY RZEDOWSKI and GRACIELA C. DE RZEDOWSKI. Instituto de Ecología, Apartado Postal 18-845, Delegación Miguel Hidalgo, 11800 Mexico, D.F., Mexico. ISBN 968-7213-02-7. 1985. 674 pp. \$35? (cloth).

The valley of Mexico is thought of as an area full of people (one of the world's largest metropolitan regions) and, therefore, quite denuded of vegetation. In reality, there is a lot of plant life in the region. The Rzedowskis are in the process of producing an excellent three volume flora of this valley: Vol. I (1979) Gymnosperms and dicots up to Polygalaceae; Vol. II (1985), the remainder of the dicots, Euphorbiaceae through Compositae (here reviewed with about 1040 species treated); Vol. III, to be published, monocots.

The format is clear and very easy to use with the families arranged in an order that seems to be of the editors' design with similarities to some modern systematic treat-

ments. This volume has a hard cover and a small but clear type face, which are distinct improvements over Vol. I that was printed by a different publisher.

The families, genera, and species are described fully with economic and distributional notes at the end of the family and generic descriptions. The species are presented alphabetically within the families except for the Compositae, which are alphabetical within the tribes. The species descriptions are concise with many unique observations, and are followed by the plant's range within the area of the flora with localities and then in general terms for its total range. A statement of the habitat and associations where the plant occurs in the valley also is given.

The keys are indented and easy to use, although some couplets in the keys to large genera are very involved, use many characters, and are a little confusing. There are good drawings with habit and details of some species in all families. One would like more, but cost and space are a valid concern.

The boundaries for this flora include the slopes of all of the various sierras that form the Valley of Mexico and range up to 5452 m. A very nice byproduct of this fact is that this flora has a utility for a much wider range, as many of the plants occur at high altitudes from Durango to Oaxaca.

Throughout the work, references are cited where they are drawn upon in the preparation of the treatments. This is reflected in the conservative and usually current species concepts presented. Although there are 46 authors of various groups in this volume alone, the presentation is uniform and reflects considerable effort by the editors to accomplish this.

The Rzedowskis are to be congratulated on the completion of this volume of the flora of the Valley of Mexico, which is a valuable addition to our knowledge of the plants of Mexico and will be a useful tool for many years to come.—DENNIS E. BREEDLOVE, Dept. of Botany, California Academy of Sciences, Golden Gate Park, San Francisco, CA 94118.

A Flora of Dry Lakes Ridge, Ventura County, California. By David L. Magney, vii + 110 pp. The Herbarium, Dept. of Biological Sciences, Univ. of California, Santa Barbara, Publication No. 5, 1986. \$8.00

This botanical research results from a four year study during every month of the year. Data include details regarding soil analyses, geology, climatology, land use, floristic history, botanical resources of special concern, environmental sensitivity, and recommendations for management procedures.

The area is north of Ojai at the headwaters of the North Fork of Matilija Creek. The ridge's north flank is drained by Sespe Creek. Access is available by foot, with some difficulty, from two directions via bulldozed firebreak/trails.

The effects on the vegetation by fires during 1932, 1948, and 1985 are explained. There are two habitat groups: 1) wetlands—consisting of stream, seeps and slopes; 2) upland—basins along the ridge at the summit with finer-grained soils.

Each principal plant species is discussed as to percentage of cover and how it dominates or persists in localized areas. Post-fire vegetation is listed. Erosion control plantings are evaluated. There are five plants endemic to the general region. Paleobotanical aspects are dealt with. Fossil evidence and woodrat middens are discussed. The book concludes with an annotated catalogue of vascular plants.

There are several black-and-white illustrations of good quality. Graphs, charts, line drawings, and maps are uncomplicated and quite understandable. The text is double-spaced and easily readable. The work is well-prepared and deals with a little-known botanical area.—WALTER KNIGHT, Research Associate, The Carnegie Museum, Section of Botany, Pittsburgh, PA.

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JAN 21	P. L. Fiedler, San Francisco State Univ. "Hierarchical thinking in rare plant biology"
FEB 20*	TO BE ANNOUNCED
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FRUIT PRODUCTION PATTERNS IN THE CHAPARRAL SHRUB *CEANOTHUS CRASSIFOLIUS*

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ABSTRACT

Annual fruit production patterns in *Ceanothus crassifolius* varied significantly over a period of six years and significant differences occurred between sites. Plants on southern exposures out-produced similar aged shrubs on northern exposures. Whether or not the causative factors are associated with aspect or differences in density of vegetative cover are unknown. Significant differences occurred among shrubs on the same slope. Some plants produced, on average, nearly an order of magnitude more fruits (per unit of areal coverage) than other plants. Fruit production patterns in *Ceanothus* species, particularly members of subg. *Cerastes*, are, in part, a function of conditions in the year prior to flowering and fruiting because flower buds are produced nearly 12 months prior to flowering. In years of heavy fruit production, internal competition for resources may limit flower bud production for the following year. This pattern is particularly likely if heavy fruit production occurs in a year of sub-normal precipitation. During the course of this study, rainfall levels were above normal in five of six years. In plants on south-facing slopes there were consecutive years of large fruit crops. Stepwise multiple regression analysis revealed that total fruit production per slope face was correlated significantly with high precipitation in February, just prior to flowering. Fruit production by individual shrubs, however, was correlated with different parameters on north-facing vs. south-facing slopes. On the former aspect, fruit production was higher in years with warmer March temperatures and on the latter aspect larger fruit crops were correlated positively with October temperature and December precipitation.

Chaparral vegetation dominates the drier slopes and foothills throughout cismontane California. Its fire-prone nature and ability to regenerate rapidly after such disturbance is well documented (Hanes 1977). Many of the dominant shrub species are capable of regeneration by vegetative sprouts from basal burls and rootcrowns, whereas others depend upon seedling establishment. Noteworthy among the latter type of shrub are the majority of species in *Ceanothus* and *Arctostaphylos*. These species have no adaptations for vegetative regeneration and are referred to commonly as obligate seeding shrubs (Wells 1969). The shrubs begin fruit production between five and 10 years of age and continue flowering and fruiting throughout their lifespan. Although seeds are dispersed soon after maturation, they remain dormant in the soil and duff until germination is stimulated by fire, or occasionally by other disturbances.

Previous studies of *Ceanothus* and *Arctostaphylos* have shown that the bulk of the seed crop is lost to predation soon after dispersal

(Keeley 1977, Davey 1982). Thus, the soil seed banks are relatively dynamic and have large fluxes in and out following dispersal of seed crops. Over long periods of time there may be relatively little increase in size of the seed banks (Keeley 1987). Consequently, postfire reproduction for obligate seeding shrubs may be tied intimately to seed production in the preceding years.

Flower and fruit production has been studied in some chaparral shrubs. In general, for both obligate and facultative seeding species of *Ceanothus* and *Arctostaphylos*, substantial fruit crops are not produced every year (Keeley 1977, Baker et al. 1982, Davey 1982, Schlesinger et al. 1982). The size and periodicity of fruit crops reported for various chaparral shrubs is highly variable and the causes for such variability are unknown. The purpose of the present study was to document fruit production patterns for one such species over a period of many years. Specific questions addressed were: 1) What is the extent of year to year variability? 2) Is this variability related to patterns of precipitation? 3) What effect does slope aspect have on fruit production patterns? 4) To what extent do individual plants vary in fruit production? and 5) Is there any relationship between the size of fruit crops in one year and the size the following year?

Ceanothus crassifolius (nomenclature for all species follows Munz 1974) was selected because it is an obligate seeding shrub and is restricted to chaparral vegetation. It is common throughout much of southern California and dominates slopes away from the immediate coast from northern San Diego Co. to San Bernardino and Santa Barbara cos. *Ceanothus crassifolius* is similar in life history to *C. megacarpus*, which was described in detail by Schlesinger et al. (1982). Seed germination and seedling establishment of *C. crassifolius* is restricted to the first spring after fire; thus, it normally forms even-aged stands. Flowering may begin as early as five years of age, although substantial flower and fruit production may not occur until 15 years of age or older. Flowering continues sporadically until the next wildfire, which typically occurs every 20–40 years in southern California.

STUDY SITES AND METHODS

Study sites. This study was conducted in the San Dimas Experimental Forest maintained by the U.S. Forest Service on the coastal front of the San Gabriel Mountains in Los Angeles Co. Two populations on north-facing and two populations on south-facing slopes with inclinations of 15–20° were selected. The slopes were on opposite sides of two east–west running ridges adjacent to Dalton Canyon Road between elevations 725 and 750 m. These stands had burned in 1960 and, thus, the plants were 17 years old at the beginning of this study in 1978.

Methods. Vegetative cover on each slope was characterized by measuring shrub coverage on each slope with two 25 m line transects. Fifteen shrubs were selected randomly on each slope and tagged. A few tagged shrubs died during the study and were replaced with adjacent individuals, so that the sample size remained the same throughout the study. Height and diameter of the nearly circular canopy were recorded in the third year of the study and did not change appreciably through the remainder of the study.

Fruit production was measured on each shrub in late spring prior to seed dispersal. A 0.25 m² hoop was placed randomly on each shrub and all fruits within the hoop were counted. This was done for six consecutive years (all sites were destroyed by a controlled burn in 1983).

Precipitation and temperature data were derived from the NOAA (1977–1983). The nearest station at this elevation with complete precipitation data was Big Tujunga Dam (710 m), which is 40 km to the west of the study site. This site, however, lacked temperature data. The Mt. Wilson Station (1740 m) had complete temperature and precipitation data and was used in the stepwise regression analysis. Although this site is at a substantially higher elevation than Big Tujunga, the yearly variations in weather patterns are similar. For example, over the period 1977–1983 monthly precipitation was correlated significantly between Big Tujunga and Mt. Wilson ($r = 0.96$, $p < 0.001$, $n = 84$).

A one-way ANOVA was used to test for differences in level of fruit production between years and among individuals on the same slope. Within a given year, a two-tailed t-test was used to test for differences between the different aspects on the same ridge and, for the same aspect, for differences between ridges. The Kendall coefficient of rank correlation analysis was used to test for a relationship between the size of the fruit crop on an individual shrub in a given year with the size of the fruit crop the following year. A stepwise multiple regression analysis was made between fruit crop size and monthly precipitation and mean temperature.

RESULTS

Cover. Total shrub coverage of all species (percentage ground surface covered) was markedly greater on the two north-facing slopes; 120% and 130% for Ridges 1 and 2, respectively, vs. 70% and 90% on the southern exposures. *Ceanothus crassifolius* comprised nearly all of the cover on the south-facing slopes, but only approximately three-fourths of the cover on the north-facing slopes. The mean height of the *C. crassifolius* shrubs was slightly more than 2.5 m on all slope faces, but generally the shrubs on the south-facing exposures had larger canopies. The largest individual shrubs were on

TABLE 1. COMPARISON OF *Ceanothus crassifolius* INDIVIDUALS ON NORTH-FACING AND SOUTH-FACING SLOPES IN THE SAN GABRIEL MOUNTAINS. Fruit production was measured on 15 individuals on each of two north-facing and two south-facing slopes for six years (slope aspects were compared with a 2-tailed t-test, ns = $p > 0.05$, ** = $p < 0.01$). Each fruit potentially can mature three seeds.

Slope aspect	Height (m) $\bar{X} \pm \text{s.d. (n)}$	Average areal cover (m ² /shrub) $\bar{X} \pm \text{s.d. (n)}$	Annual fruit production (fruits/m ² areal coverage) $\bar{X} \pm \text{s.d. (n)}$
Ridge 1			
North	2.5 \pm 0.3 (15) ns	3.0 \pm 2.5 (15) **	284 \pm 497 (90) **
South	2.6 \pm 0.3 (15)	7.9 \pm 3.4 (15)	576 \pm 515 (90)
Ridge 2			
North	2.6 \pm 0.6 (15) ns	2.2 \pm 1.0 (15) ns	223 \pm 515 (90) **
South	2.6 \pm 0.3 (15)	3.2 \pm 2.1 (15)	386 \pm 405 (90)

the south face of Ridge 1, which was the most open of the four slope faces.

Fruit production. Due to the different sizes of shrubs on these slopes, fruit production is expressed on an areal coverage basis. Averaged over the six years of this study, the number of fruits produced per m² of areal coverage was significantly greater on south-facing exposures than on north-facing exposures (Table 1). Level of fruit production was similar between the two north-facing slopes, but the south face of Ridge 1 had significantly greater annual fruit production than that exposure on Ridge 2 ($p < 0.01$). Because there was much plant to plant variation and yearly variation in size of fruit crops, the variance in fruit production was generally high on all slopes (Table 1).

Annual patterns of fruit production are illustrated in Fig. 1. For all exposures there was a significant difference in fruit production between years. For all slopes, 1978 was a year of high fruit production and, for the south-facing exposures, this was followed by another year of high fruit production. The shrubs on the southern exposures significantly ($p < 0.01$) out-produced shrubs on the northern exposures in all years except 1978 on Ridge 1 and 1979, 1982, and 1983 on Ridge 2. In all years, fruit production between the two north-facing slopes was not significantly different ($p < 0.05$). In 1980 and 1981, production on the south-facing slope on Ridge 1 was significantly higher than the same exposure on Ridge 2 ($p < 0.01$).

Within a given year the variation in fruit production between plants on a single slope was high; the coefficient of variation usually

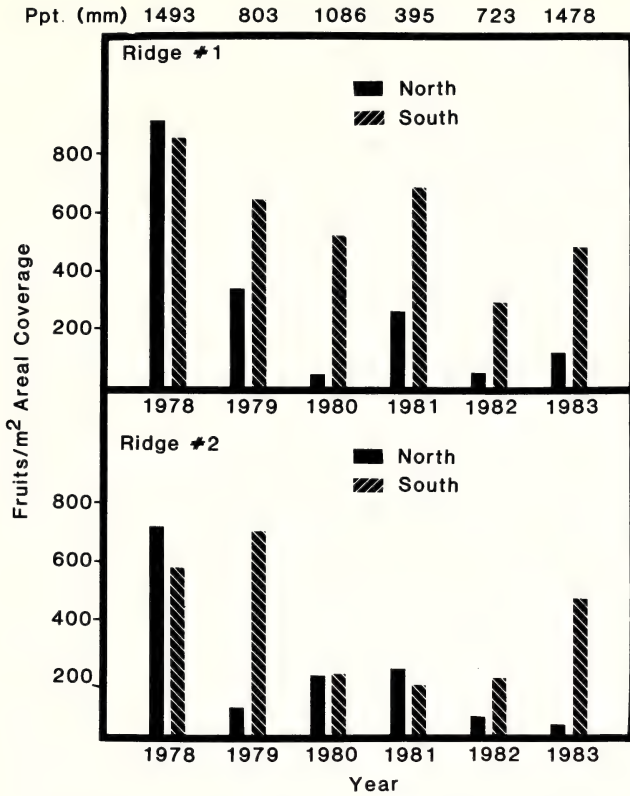


FIG. 1. Annual fruit production for years 1978–1983 for *Ceanothus crassifolius* on north- and south-facing exposures in Dalton Canyon in the San Gabriel Mountains of southern California ($n = 15$ shrubs per slope). Statistical analyses are given in the text. Precipitation data is for the period July–June and is from Big Tujunga Dam; average = 660 mm per year.

exceeded 80% and often was above 100%. During the period of this study there was a significant difference between individuals on the south face of Ridge 1 ($p < 0.01$). On this slope, over the six-year period, one shrub averaged 1140 ± 747 fruits m^{-2} areal coverage per year whereas another produced nearly an order of magnitude fewer (173 ± 80 fruits m^{-2} areal coverage). On the other slopes, there was much variation in size of fruit crops, but across all six years there was no significant difference among shrubs.

An analysis of the size of the fruit crop on an individual shrub in a given year with the size in the following year showed that there was a significant positive relationship in fruit production between 1978 and 1979, and between 1980 and 1981 ($p < 0.01$). Thus, for

those years, shrubs on south-facing slopes that produced the largest fruit crops in 1978 and 1980 produced the largest crops in the succeeding year. Shrubs on the northern exposure showed no significant correlation between any years.

Precipitation and temperature patterns. During the course of this study, five of the years had above average precipitation levels (Fig. 1). The year of highest fruit production, 1978, was also the year of highest precipitation (the 1977–1978 rainfall season had more than double the average). There also was much greater than average rainfall during the 1982–1983 season, yet fruit production, particularly on north-facing exposures, was not high in 1983. In three years of this study the summer drought was interrupted by measurable precipitation resulting from unusual subtropical storms; >30 mm precipitation was recorded in either August or September of 1977, 1978, and 1982. On south-facing slopes these were followed by years of high fruit production.

A stepwise multiple regression analysis was made between annual fruit crop size and precipitation and mean temperature for all months from March of the previous year through June of the year of the fruit crop, and including annual precipitation total as well as summer, fall, winter, and spring precipitation totals. There was a highly significant positive correlation between the mean fruit crop size per slope and February precipitation ($r = 0.61$, $p < 0.005$, $n = 24$). However, this relationship did not hold up if slopes were compared separately. Using fruit crop size for each shrub on the two north-facing slopes revealed that only March temperature was positively correlated with fruit crop size ($r = 0.52$, $p < 0.001$, $n = 180$). On the south-facing slopes, the stepwise regression included both October temperature and December precipitation ($r = 0.35$, $p < 0.001$, $n = 180$), both of which were positively correlated with fruit crop size.

DISCUSSION

Annual variation in fruit production by chaparral shrubs is likely dependent upon environmental conditions during the season of flowering and fruiting. Flower production by species of *Ceanothus* (subg. *Cerastes*) also may be dependent upon conditions during the previous growing season. This is because flower buds are produced at the end of the previous year's growing season, and as a consequence, flowering is on old growth branchlets (Keeley 1977, Kummerow et al. 1981; found in all species of subg. *Cerastes*, although not easily recognized, cf. Baker et al. 1982).

I propose a model in which fruit production is a function of the number of nascent flower bud primordia produced at the end of the previous growing season, flowering success, and the level of pho-

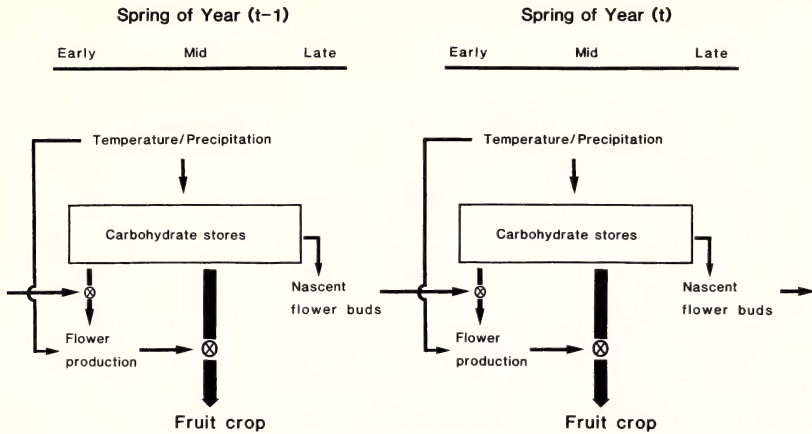


FIG. 2. Schematic model of factors influencing the size of fruit crops in *Ceanothus* species. Fruit production in year (t) will be a function of the number of nascent flower buds produced the previous year ($t - 1$), flowering success, and the level of carbohydrates available during fruit maturation.

tosynthates available during fruit maturation (Fig. 2). This model may be useful for interpreting annual fruit production patterns in other chaparral shrubs that produce floral primordia in the year prior to fruiting [viz., all species of *Arctostaphylos*, *Garrya*, and *Rhus*, excluding *R. (Malosma) laurina*, Keeley unpubl. data].

In the model, nascent flower bud production is a function of the level of carbohydrate stores available at the end of the growing season and carbohydrates are a function of photosynthate production and demands by carbohydrate sinks. Photosynthate production by chaparral shrubs is insensitive to annual variations in temperature relative to the role of soil moisture (Oechel et al. 1981). Thus, in years of high precipitation, carbohydrate production should be higher than in years of low precipitation. Carbohydrate sinks include growth and maintenance as well as fruit production. The latter represents a substantial, and annually variable, carbohydrate drain. Because *Ceanothus* flower buds arise from axillary meristems in the nodes of leaves, nascent flower bud production also would be an indirect function of the extent of terminal branch and leaf production during that growing season.

Flower production should be a function of the number of nascent flower buds produced the previous year and the available carbohydrate stores present at the time of flowering. Because flowering takes place in early spring, temperature, through its effect on pollinators, presumably plays a role in determining success.

Although I recognize that other factors are involved, I suggest that this model is conceptually useful in understanding annual variation

in size of fruit crops observed for species of *Ceanothus*. For example, in a study of *C. greggii* in San Diego Co. massive fruit crops were reported for 1974 (Keeley 1977), a year with a 60% precipitation deficit (all references to annual precipitation are for the rainfall season, in this instance 1 Jul 1973 to 30 Jun 1974, most of which falls in winter and spring). The considerations discussed above would predict that 1) the 1973 season should have had high precipitation (requisite for flower bud production), and 2) poor fruit production in 1975 (due to limited flower bud production in 1974, a consequence of high fruit production combined with limited precipitation in 1974); both of these predictions were true. A four-year study of *C. megacarpus* in Santa Barbara Co. reported that the highest fruit production occurred in 1978, which was a year of very high rainfall (Schlesinger et al. 1982). Although it followed a year of subnormal precipitation, massive flower bud production in 1977 apparently was possible as a result of a lack of fruit production that year. This pattern was seen also for *C. crassifolius* in the present study, where the year of highest fruit production (1978) was preceded by a year of subnormal precipitation, but also one in which fruit production was low (reported by Davey in 1982 for a nearby site).

It is also apparent that on different slope faces fruit production may be sensitive to different environmental factors. Higher March temperatures are correlated with higher fruit production on north-facing slopes. March is the peak month for flowering and, thus, warmer temperatures may be critical to pollinator success on these cooler north-facing slopes. On south-facing sites, higher fruit production is correlated with higher December precipitation and October temperatures. These factors may affect seasonal carbon gain and, thus, overall carbohydrate stores on these south-facing slopes.

One implicit factor in the model (Fig. 2) is the effect of summer and fall drought on nascent flower bud survival. Baker et al. (1982) suggested this to be an important factor controlling fruit production in *Arctostaphylos*. Bud survival might be affected by total seasonal precipitation and also by atypical summer thunderstorms. As noted here, significant summer precipitation occurred in 1977, 1978, and 1982, and these years were followed by high fruit production on south-facing slopes.

An understanding of the factors responsible for temporal variation in fruit production is complicated in that there is significant spatial variation (Fig. 1). Throughout this investigation, the shrubs on southern exposures out-produced those on northern exposures. The regression analysis suggests that cooler temperatures during flowering may play a role in controlling fruit production on north-facing slopes. Soil moisture levels, however, may play a role because results from other studies would predict higher soil moisture levels for the sparsely vegetated south-facing slopes (Poole et al. 1981).

Elevational differences also may affect level of fruit production. Davey (1982) documented *C. crassifolius* seed production on a south-facing slope (last burned in 1960) within 1 km of my sites, but at approximately 200 m higher elevation. For the years 1978–1980, she reported seed fall of 6000–8000 seeds m^{-2} ground surface, which for her sites translates into 4000–5500 seeds m^{-2} areal coverage. Assuming each fruit dispersed the maximum number of seeds possible (i.e., three), the highest seed fall observed at my sites during those same years would have been 1500–2500 seeds m^{-2} areal coverage.

Even within a site there is much interplant variation. On the south-facing exposures studied here, some shrubs out-produced (by an order of magnitude) others that were only meters away. That some shrubs consistently produced larger fruit crops than others nearby suggests either inherent genetic differences in shrubs, or important microhabitat differences. Small scale differences in soil depth could produce different soil moisture regimes (Miller and Hajek 1981); however, nothing is known about the subsoil conditions at these sites.

More and longer term studies of fruit production will be needed before we can elucidate all factors responsible for the annual variation in magnitude of fruit crops in these chaparral shrubs. Future studies will need to consider microhabitat characteristics and other environmental parameters in order to fully account for fruit production patterns in these species.

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ANNOUNCEMENT

SANTA CRUZ ISLAND RESEARCH PROJECTS

The Nature Conservancy (TNC) proposes a number of research questions for which they would like to receive proposals for funding. Projects will be funded by the Santa Cruz Island Research Fund jointly administered by the Santa Barbara Museum of Natural History and The Nature Conservancy. The projects should address the specific question(s) and provide management recommendations. All projects with management recommendations should include a section on the possible impacts and effects that mitigation measures might have on current operations of the Santa Cruz Island Company. The inclusion of recommendations does not imply that TNC will act upon them in the immediate future.

The list of questions is divided into two categories: projects dealing with general baseline studies and inventories of widespread general utility, and projects dealing with immediate biological and/or management concerns. We will review all proposals and grant funding on the merit of the individual project and the appropriateness of the topic to the Conservancy's needs. Several projects have potential for collaboration with the Channel Islands National Park Service or for contributing new data to the established geographical information system.

For a copy of the list of research questions or for more information, contact the Preserve Director, Peter Schuyler, Santa Cruz Island Project, 213 Sterns Wharf, Santa Barbara, CA 93101.

SEED DISPERSAL IN *CEANOOTHUS CUNEATUS*
AND *C. LEUCODERMIS* IN A
SIERRAN OAK-WOODLAND SAVANNA

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ABSTRACT

Seed dispersal of *Ceanothus cuneatus* and *C. leucodermis* was studied in an oak-woodland community in the central Sierra Nevada of California. As the capsule of *Ceanothus* (usually containing three seeds) matures and dries, it opens with force and ejects its seeds at varying distances. Seed-casting, in relation to date, showed a skewed polynomial distribution that peaked early in July and gradually tapered off. The active seed-casting period lasted two weeks in the one year of study. Phenology of fruit ripening, temperature, and humidity were related directly to time and rate of seed-casting. About one-third of the seeds fell beneath the canopy, whereas the remainder were cast away from the shrub in an exponential density distribution. Forty-two percent of the seeds (average density of 2850 m^{-2}) fell at the edge of the shrub and 1.9% (average density of 10 m^{-2}) at 9 m. The probabilities that seeds would be cast within specific distances from the shrub were 29% (at the edge of the shrub to 2 m), 33% (4–6 m), and 21% (8–9 m).

Ceanothus comprises 55 species restricted to North America, and most are found along the Pacific coast of the United States (Reed 1974). Californian species are ecologically diverse and, among other communities, are found in the chaparral, oak-woodland savannas, and lower coniferous forests of the Sierra Nevada. *Ceanothus* is important as wildlife feed and habitat, and because of its nitrogen-fixing properties also is important in soil development and conservation (Zavitkovski and Newton 1968, Youngberg and Wollum 1976). Among the oak-woodland savannas of the Sierra Nevada foothills, *C. cuneatus* and *C. leucodermis* are considered weeds to livestock producers because they compete with the herbaceous vegetation and reduce the yield of forage for cattle (Biswell 1974).

As the capsule of *Ceanothus* matures and dries, it opens with force and ejects the seeds to varying distances from the parent shrub. Explosively dispersed seeds have been reported for other genera, including *Dendromecon*, *Oxalis*, *Viola*, *Phlox*, *Geranium*, *Alstroemeria*, *Lupinus*, *Impatiens*, *Millettia*, and *Hura* (Swaine and Beer

1977). Individuals of these genera cast their seeds 1–45 m, depending on species and size of plant. Little is known about the advantages of explosive seed dispersal in terms of seed germination or plant establishment. Many questions remain unanswered about the adaptive advantages conferred on a species by investment in dispersal structures (Howe and Smallwood 1982).

The primary objectives of this study were to investigate seed dispersal patterns of *C. cuneatus* and *C. leucodermis* in order to more fully understand seed bank characteristics that appear advantageous to the establishment of new plants, and to examine seed dispersal patterns in light of theoretical models of explosively dispersed seeds (Beer and Swaine 1977) and the theoretical distribution and probability distributions of seeds (Peart 1985).

METHODS

Studies were conducted in a California oak-woodland savanna community, situated in the foothills of the central Sierra Nevada, 70 km northeast of Fresno, at 910 m and with an average rainfall of 760 mm. Dominant tree species are *Pinus sabiniana*, *Quercus douglasii*, *Q. wislizenii*, and *Aesculus californica*, and dominant shrub species are *Ceanothus cuneatus* and *C. leucodermis*. An understory of herbaceous plants includes the annual grasses, *Bromus mollis*, *B. diandrus*, *B. rubens*, *Avena barbata*, *A. fatua*, and *Festuca* spp.; and the broadleaf plants, *Erodium botrys*, *E. cicutarium*, *Medicago polymorpha*, and *Trifolium* spp.

Eight representative plants of *Ceanothus cuneatus* and *C. leucodermis* were selected in the study area (*C. cuneatus*, 1–3.5 m tall and *C. leucodermis*, 2–4 m tall; Munz 1973). Transects 10 m long and 0.6 m wide, radiating out in eight compass directions from two large shrubs, one of each species, were cleared of herbaceous vegetation and plant litter (Fig. 1). One meter intervals along the transects were marked by large nails beginning at the edge of the shrub canopy. There was one sampling point beneath the canopy on each transect positioned 0.3 m inside the canopy edge. On smaller shrubs, one to four transects were made along compass directions radiating out from each shrub, based on the proximity of adjacent shrubs and terrain. These transects were cleared and marked in a similar fashion to the large shrubs. No transects were made adjacent to neighboring shrubs to avoid measuring areas of overlap of seed dispersal from two or more shrubs.

Sampling for seed dispersal consisted of counting seeds within a 0.1 m² frame every other day during the active casting period. After seeds were counted, the transects were swept clean with a whisk broom. The counts were made in early evening or early morning when seeds were not dehiscing. To minimize seed predation, ants



FIG. 1. *Ceanothus cuneatus* with cleared transects radiating out from the shrub in eight cardinal directions.

were poisoned in the transect areas. No indication of seed predation by rodents or birds was noted during the course of the study.

When the capsules of *Ceanothus* burst open and dehisce their seeds an audible pop is heard. At the height of casting on 20 July, seed dehiscing on the large shrubs of both species was monitored every 30 minutes from 0700–2130 hr by counting the number of pops heard by an observer standing close to the individual shrub for three 60 second intervals. At the same time, measurements of relative humidity and temperature were made using a sling psychrometer. Seasonal weather data were taken from the nearest station, North Fork Ranger Station, located 16 km south of the study area at 800 m.

Results were analyzed statistically by ANOVA with Duncan's multiple range test to determine differences in seed density in relation to compass direction. Correlation and curvilinear regression techniques were used to portray and analyze seed dispersal relative to distance from the shrub canopies and to calendar date.

RESULTS

Seed-casting in relation to date. Seed-casting for both *C. cuneatus* and *C. leucodermis* occurred from 13 July to 11 August 1952. The

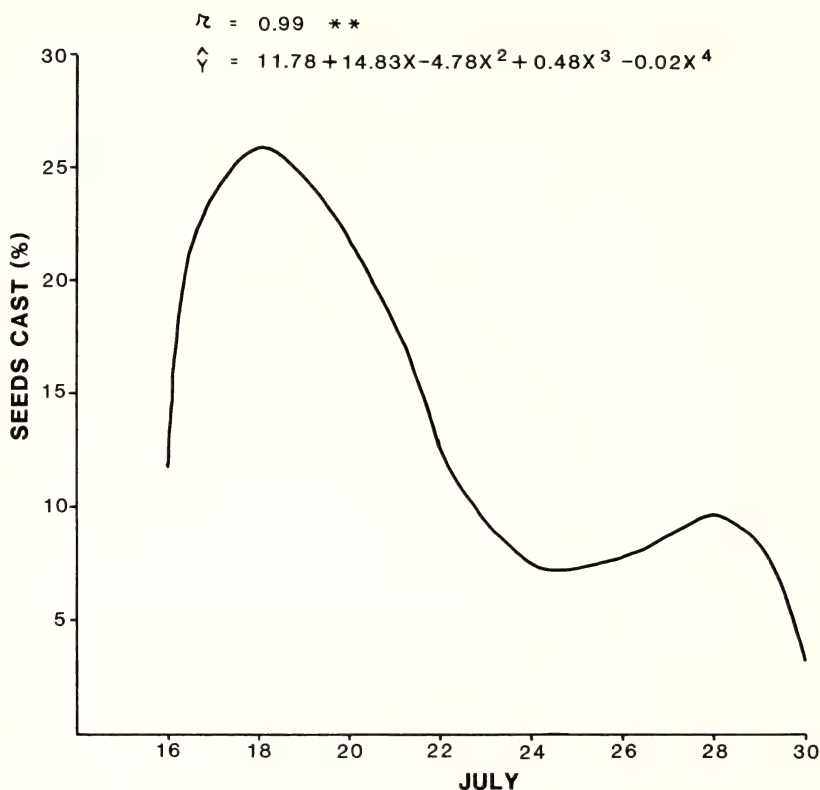


FIG. 2. Fourth-degree polynomial distribution curve of percentage of *Ceanothus cuneatus* seeds cast in relation to calendar date. Multiple correlation coefficient (r) is significant at $p \leq 0.01$.

period of active seed-casting, when more than 95% of the observed total seeds were dispersed, lasted 14 days (16–30 July). Average maximum and minimum daily temperatures during active seed casting were $35.7 \pm 2.1^\circ\text{C}$ and $15.1 \pm 2.5^\circ\text{C}$, respectively. Rain showers occurred 25 July (2.3 mm) and 30 July (2.5 mm). Partly cloudy weather accompanied the showers, which increased the humidity and decreased air temperatures during these periods.

Maximum seed-casting occurred on 18 and 20 July (two and four days after the active seed-casting period began) for *C. cuneatus* and *C. leucodermis*, respectively (Figs. 2, 3). Seed casting in relation to date formed a skewed fourth-degree polynomial distribution in which the numbers of seeds cast increased rapidly from the initiation of casting and decreased gradually over the following 10–12 days. In *C. cuneatus*, a marked decrease in seed dispersal was noted during

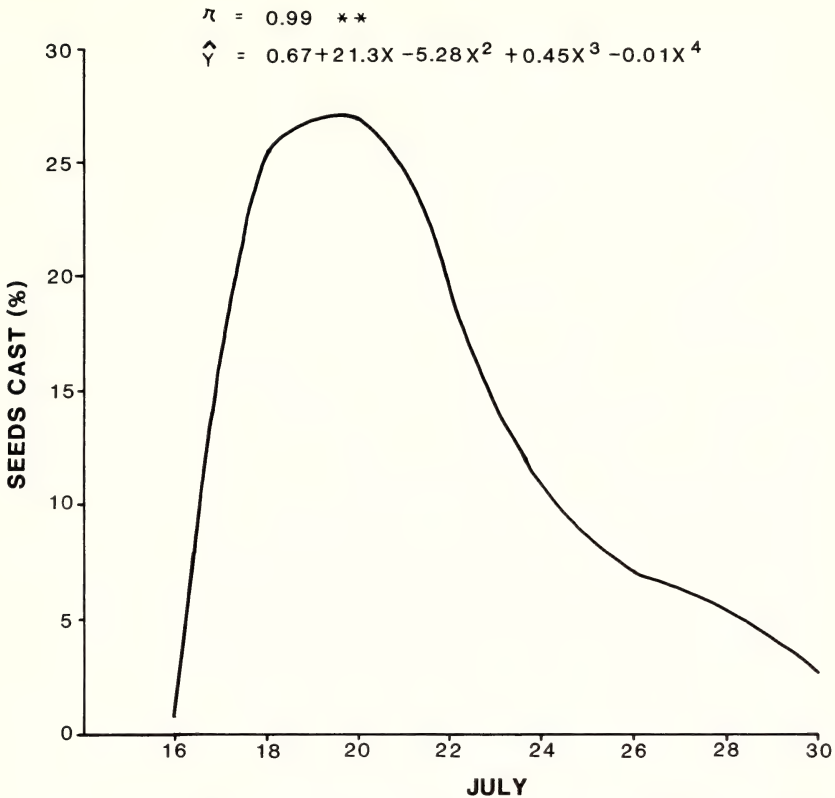


FIG. 3. Fourth-degree polynomial distribution curve of percentages of *Ceanothus leucodermis* seeds cast in relation to calendar date. Multiple correlation coefficient (r) is significant at $p \leq 0.01$.

the period of higher humidity and rainfall toward the end of active seed casting and then a subsequent increase with higher temperatures and lower humidity (Fig. 2). In *C. leucodermis*, this response was similar, but of less magnitude (Fig. 3).

Seed-casting in relation to time of day. On 20 July, seed casting of both species occurred from 0930–2130 hr (Fig. 4). Seed-casting in *C. cuneatus* reached a maximum at 1200 hr and continued at a high level (20/min being counted) until 1700 hr. Seed-casting in *C. leucodermis* increased to a high level at 1230 hr and reached similar maxima at 1730 and 1830 hr. Total seeds cast on 20 July was almost identical for monitored shrubs of both species (Figs. 2, 3). At the onset of seed-casting, temperature was 27°C and relative humidity (RH) 30%. In the most active period of seed-casting, temperatures

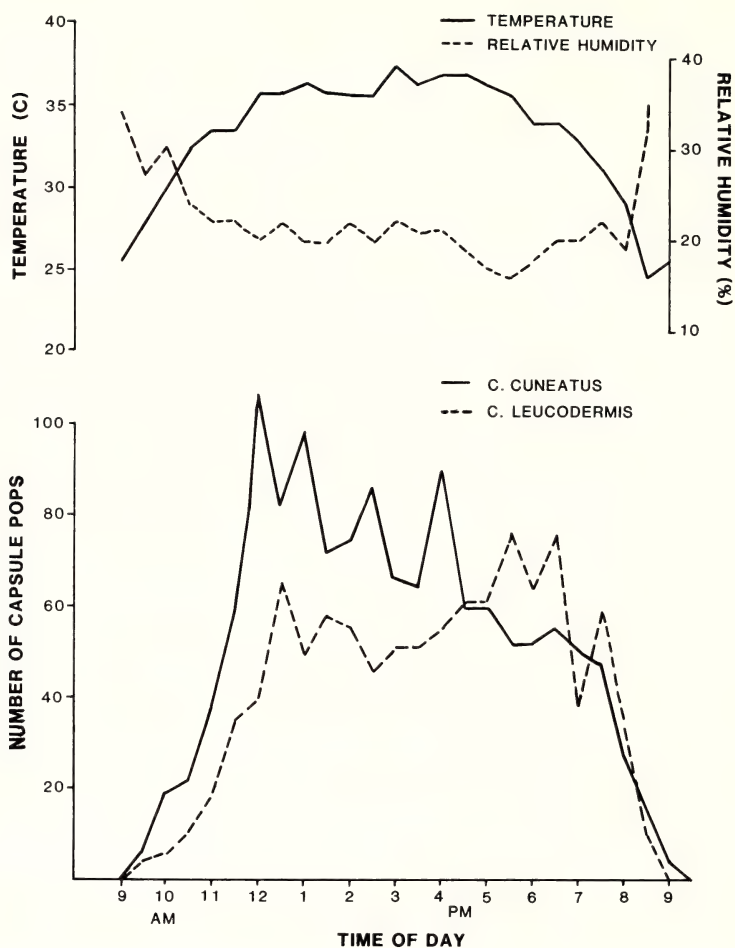


FIG. 4. Number of capsule pops of *Ceanothus cuneatus* and *C. leucodermis* per three minute period and air temperature and relative humidity for each one-half hour on 20 July.

ranged from 35–38°C with RH from 15–20%. At cessation of casting, temperature was 25°C and RH was 37%.

Seed-casting in relation to distance from shrub. Of the total seeds cast, 32% and 36% fell beneath the shrub canopy of *C. cuneatus* and *C. leucodermis*, respectively. This presumably resulted from seeds striking branches or leaves or because the seed capsules were oriented downward or inward. The remainder of seeds cast by both species formed an exponential density distribution from a high of 42% at the edge of the shrub to 1.9% at 9 m from the shrub (Fig. 5). Seed

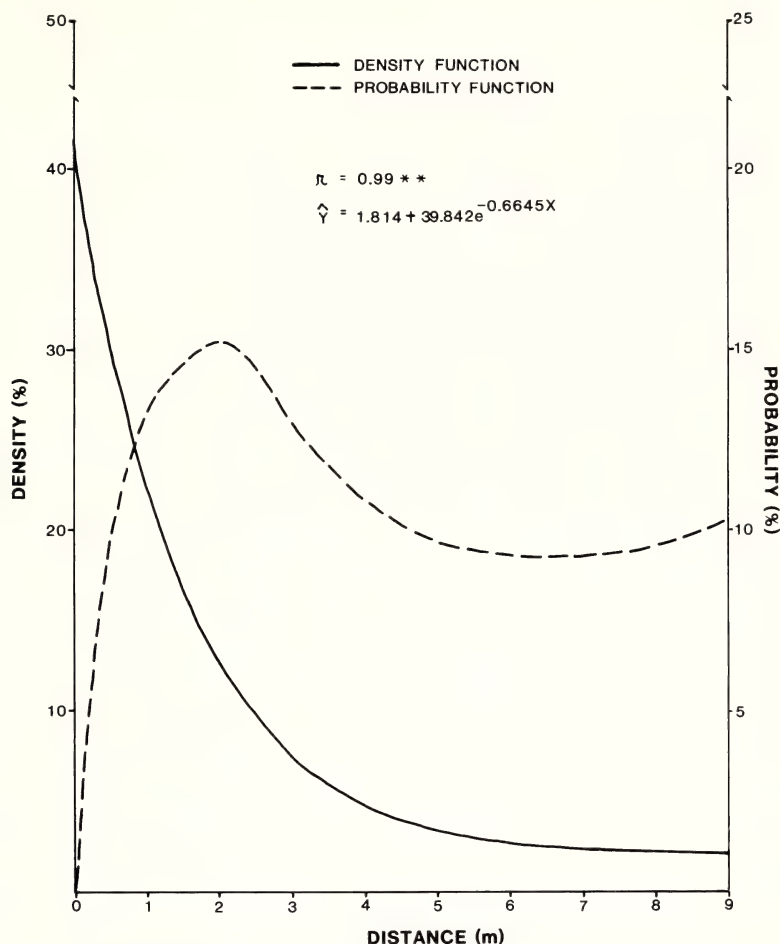


FIG. 5. Density and probability functions of seed-casting distribution of *Ceanothus cuneatus* and *C. leucodermis* in relation to distance from edge of the parent shrub. Data for both species are combined. Multiple correlation coefficient (r) of the density function is significant at $p \leq 0.01$. Probability function should be interpreted as a measure of probability of a seed landing within a specific distance range from edge of the parent shrub.

densities averaged 2850 m^{-2} at the edge of the shrub to 10 m^{-2} at 9 m. Overall dispersal patterns of different shrubs were consistent in both species and were not significantly different ($p \leq 0.05$) between species (Table 1). Highest seed densities, those near the shrubs, agreed with densities reported by Keeley (1977) for *C. leucodermis*.

The probability of a seed escaping from the parent plant and landing within a specific distance range was derived by $P(r) =$

TABLE 1. CALCULATED SEED DENSITIES OF *Ceanothus cuneatus* AND *C. leucodermis* AT VARIOUS DISTANCES FROM THE PARENT SHRUBS WITH CONFIDENCE INTERVALS DERIVED FROM MULTIPLE REGRESSION. Correlation coefficient for multiple regression = 0.99; n = per 0.1 m².

Distance from edge of shrub (m)	<i>C. cuneatus</i> (n)	<i>C. leucodermis</i> (n)	Confidence interval p = 0.05
0	273	277	16
1	163	167	10
2	92	96	8
3	53	57	8
4	31	35	8
5	19	23	8
6	16	8	9
7	8	12	9
8	6	10	9
9	5	9	9

$2\pi rD(r)dr$ (Peart 1985), where $P(r)$ = probability of a seed escaping to an angular area at distance (r) from the point of release; $D(r)$ = a density-dispersal function based on actual sampling data of the two species; and dr = sample size of 0.1 m. Results indicated that the probability of a seed landing within specific distance ranges from the parent shrub varied from 29% (edge of the shrub to 2 m), to 33% (4–6 m), and to 21% (8–9 m) (Fig. 5).

Seed-casting in relation to direction from shrub. Over the active period of casting, most *C. cuneatus* seeds were cast in a southwesterly direction and fewest in a westerly direction. Early in the casting period and at maximum seed dispersal more seeds were cast to the north and east, whereas later in the casting period most seeds were cast in the southwesterly direction. In *C. leucodermis*, most seeds were cast in a southeasterly direction and fewest were cast in a westerly direction. Most seeds were cast to the southeast during the 10 days of most active seed dispersal. In both species, fewer seeds were cast to the west throughout the dispersal period (Table 2).

DISCUSSION

Seed-casting in *Ceanothus cuneatus* and *C. leucodermis* occurs during a short but active period (14 days in this study), when the capsules ripen and expel their seeds (usually three per capsule) to a distance of 9 m or more. Seeds are dispersed mainly beneath or near parent shrubs, but explosive dispersal permits a wider distribution of some seeds. Both diurnal and seasonal trends of seed-casting seem to indicate that specific thresholds of temperature and moisture were critical for seed-casting in *Ceanothus*. Our results suggest that commencement and rate of seed-casting are functions of the phenological

TABLE 2. PERCENTAGE OF SEEDS CAST IN DIFFERENT DIRECTIONS FROM PARENT SHRUBS OF *Ceanothus cuneatus* AND *C. leucodermis*. Values followed by the same letter are not significantly different at the 0.05 level of probability as determined by Duncan's multiple range test. All comparisons are made horizontally within species.

Species	Compass direction							
	n.	ne.	e.	se.	s.	sw.	w.	nw.
	Percent							
<i>C. cuneatus</i>	10.7ab	10.9ab	13.6ab	12.6ab	15.0ab	15.6a	7.6b	14.0ab
<i>C. leucodermis</i>	12.9ac	10.0bc	8.8c	15.9a	15.0ab	13.1a-c	10.0bc	14.3ab

stage of fruit ripening and of the temperature and relative humidity as they affect plant moisture status.

Ceanothus seeds require relatively high temperatures (70–100°C) for germination (Reed 1974). Most germination and seedling establishment is associated with fire (Quick and Quick 1961, Schlesinger and Gill 1978). Between fires, large seed banks of *C. cuneatus* and *C. leucodermis* beneath and around shrubs can accumulate in the Sierran oak-woodland savanna.

Effects of the interaction of seed dispersal at varying distances from the parent shrubs and seed mortality in relation to fire temperature as influenced by type (shrub vs. herbaceous) and amount of fuel create a mosaic of safe sites (Harper et al. 1965) for seed germination and plant establishment. Seedling establishment of *Ceanothus* in relation to competition from herbaceous species (Schultz et al. 1955) that grow among shrubs increases heterogeneity of the seed bank in terms of safe sites and restricts opportunities for successful establishment of seedlings. Furthermore, wide dispersal of long-lived seeds of *Ceanothus* increases the probability for establishment of new plants by reducing the effects of seed predation by insects, predation and herbivory by rodents, and intraspecific seedling competition (Peart 1985).

ACKNOWLEDGMENTS

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ANNOUNCEMENT

THE 1987 JESSE M. GREENMAN AWARD

The 1987 Jesse M. Greenman Award has been won by Geoffrey A. Levin for his publications "Systematic Foliar Morphology of Phyllanthoideae (Euphorbiaceae). I. Conspectus", "Systematic Foliar Morphology of Phyllanthoideae (Euphorbiaceae). II. Phenetic Analysis", which appeared in the *Annals of the Missouri Botanical Garden*, volume 73, number 1, and "Systematic Foliar Morphology of Phyllanthoideae (Euphorbiaceae). III. Cladistic Analysis", which was published in *Systematic Botany*, volume 11, number 4. This series of papers is derived from a Ph.D. dissertation from the University of California, Davis, under the direction of Drs. James A. Doyle, Grady L. Webster, and Jack A. Wolfe. Dr. Levin uses a large set of characters (in this case leaf characters) to address questions of systematic relationships and phylogeny at higher taxonomic levels, using the results from both phenetic and cladistic analysis to evaluate a more traditional classification system, and to identify genera or groups of genera whose position and relationship are not clear and, therefore, are in need of additional study.

The Award is named for Jesse More Greenman (1867-1951), who was Curator of the Missouri Botanical Garden Herbarium from 1919 until 1943. A cash prize of \$250 is presented each year by the Garden, recognizing the paper judged best in vascular plant or bryophyte systematics based on a doctoral dissertation that was published during the previous year. Papers published during 1987 are now being considered for the 20th annual award, which will be presented in the summer of 1988. Reprints of such papers should be sent to: Greenman Award Committee, Division of Research, Missouri Botanical Garden, P.O. Box 299, St. Louis, MO 63166-0299, U.S.A. In order to be considered for the 1988 award, reprints must be received by 1 June 1988.

SEEDCROP CHARACTERISTICS AND MINIMUM REPRODUCTIVE SIZE OF ORGAN PIPE CACTUS (*STENOCEREUS THURBERI*) IN SOUTHERN ARIZONA

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ABSTRACT

Seedcrop characteristics and the relationship of reproductive activity to size of organ pipe cactus (*Stenocereus thurberi*) were examined in Organ Pipe Cactus National Monument, Arizona. A sample of 19 fruits collected had a mean diameter of 52.9 mm and a mean seed content of 1969 seeds/fruit. Laboratory germination percentage at 20–25°C and a 12 hr photoperiod was 88%. Height measurements and fruit presence/absence observations made at two locations in the Monument indicate that most *S. thurberi* individuals begin to reproduce when they are 2–2.5 m in height. Plants typically have 4–10 arms by the onset of reproductive maturity. Large individuals of *S. thurberi* may produce more than 50 fruits in a season. These results indicate that the reproductive potential of mature individuals of this species is high.

The giant cactus forests of the Southwest have captured the interest of botanists and travelers to that region for over a century. Although three of the columnar cactus species found in the Sonoran Desert occur naturally in the United States, the vast majority of scientific studies on columnar cactus conducted in this country (e.g., Shreve 1910, Niering et al. 1963, Steenbergh and Lowe 1969, 1977, 1983) have focused on saguaro [*Carnegiea gigantea* (Engelm.) Britt. & Rose], the most widespread and conspicuous of the columnar cacti in the United States. In favorable habitats, organ pipe cactus [*Stenocereus thurberi* (Engelm.) Buxb.] (Fig. 1) also is prominent, but its range within the United States is restricted to several populations in southern Arizona (Hastings et al. 1972). It has received much less attention from scholars than *C. gigantea*; consequently, we know less about the basic ecology and population dynamics of *S. thurberi* than of *C. gigantea*. Recent studies have begun to identify ecological characteristics (Nobel 1980, Smith et al. 1984) and site preferences (Yeaton and Cody 1979) of *S. thurberi* in the northern part of its range, but McDonough's (1964) study of factors affecting seed germination is the only work published on the reproductive characteristics of this species.

The purpose of this study was to determine the size at which individuals become reproductively active and the fruit size and seed production and germinability for populations of *S. thurberi* in southern Arizona.



FIG. 1. Fruiting individual of *Stenocereus thurberi* in Organ Pipe Cactus National Monument.

METHODS

Study area. The study was conducted in Organ Pipe Cactus National Monument (OPCNM), which supports one of the most extensive populations of *S. thurberi* in the United States. Data were collected in late June and early July 1976, approximately midway

through the flowering and fruiting season for reproductively active plants.

Mean annual precipitation at the Monument headquarters is 233 mm (Weather Bureau 1951–1974, NOAA 1975–1980), although data from a network of backcountry raingauges indicate that rainfall is generally higher in the Ajo Mountains along the eastern boundary of the Monument because of orographic uplift (Table 1). For the 17 yr period from 1962–1983 (exclusive of 1967 and 1973–1976 when backcountry records were incomplete), annual rainfall at a remote station in the Ajo Mountains exceeded rainfall at the official weather station in the Monument by a mean value of 101 mm (s.d. = 148 mm, range = –45 to 418 mm). Precipitation is distributed bimodally throughout the year, with the primary rainfall maximum coinciding with the time of fruit maturation during summer and the secondary maximum occurring during winter. Annual precipitation for the year prior to the study (1975) was well below the mean, and the summer of that year was the driest of the last 35 yr (1950–1984; Table 1).

Nocturnal freezes occur occasionally in the Monument (\bar{X} = 19 freezes/year; Table 1), but no subfreezing daily maximum has been recorded at the Monument headquarters in its 42 yr history as a weather station. The winter preceding the study (1975–1976) had a typical number of freezes, with -5°C as the lowest temperature recorded that winter.

Sample sites. To analyze the relationship between size and reproductive activity, data were collected from two sites within OPCNM that had similar slope characteristics. Both were on south–southwest-facing rocky hillsides with slope angles from $15\text{--}20^{\circ}$ and approximately 25–50 m above the the adjacent valley floor. Both valleys sloped gently southward as part of the Sonoyta River drainage network. Soils in both sites were shallow gravelly loams. The Twin Peaks site ($31^{\circ}57'\text{N}$, $112^{\circ}49'\text{W}$) was located north of the Monument campground (within 2 km of the weather station) on the lower slopes of Twin Peaks between 1740–1800 m. The site was sampled with ten 7×50 m rectangular quadrats. The Ajo Mountain site ($32^{\circ}00'\text{N}$, $112^{\circ}42'\text{W}$) was located on the lower slopes of the Ajo Mountains from 2120–2200 m (within 2 km of the backcountry raingauge in the Ajo Mountains). This site was sampled with three 7×50 m quadrats. The area sampled was smaller for the Ajo Mountain site because there was less homogeneous habitat available for quadrat placement than in the Twin Peaks site. For all individuals within the sampling quadrats, the height of the tallest arm, the number of arms, and the presence or absence of buds, flowers, or fruits were recorded.

Fruit and seed samples. Nineteen ripe fruits were collected from *S. thurberi* plants within the two study sites. Each fruit was taken

TABLE 1. CLIMATIC SUMMARY AND CONDITIONS IN THE YEAR PRIOR TO STUDY IN ORGAN PIPE CACTUS NATIONAL MONUMENT. Means and standard deviations (s.d.) for the official station (near Twin Peaks) are calculated for the period 1951–1980 with data published by the Weather Bureau (1951–1974) and NOAA (1975–1980); mean and s.d. for freeze frequency are based on the 29 yr period excluding 1980 because of missing data. The previous year is defined as 1975 for annual and summer precipitation and as the winter of 1975–1976 for the number of freezes/winter. Mean and s.d. for the Ajo Mountains are based on data from a backcountry rain gauge monitored by the Monument staff for the period 1962–1983 (exclusive of 1967 and 1973–1976).

	Official station			Ajo Mountains	
	$\bar{X} \pm \text{s.d.}$	Range	Pre- vious year	$\bar{X} \pm \text{s.d.}$	Range
Annual precipitation (mm)	233 \pm 78	87–377	111	342 \pm 154	132 \pm 657
Summer precipitation (mm) (June– September)	107 \pm 56	17–192	17	—	—
Freezes/winter	19 \pm 7	5–34	20	—	—

from a different individual. After removal of any persistent spines and dried flower parts, fruit lengths and maximum diameters were measured with a dial caliper graduated by 0.05 mm. Fruits were weighed with a triple beam balance immediately after collection. Seeds were then separated from the flesh of the fruits with a sieve. Seeds were air dried and weighed, and the number per fruit was determined. Seeds were stored for about 30 days in the dark at 20–25°C before they were used in germination tests.

Seed germinability was determined on a random sample (100 seeds) of those collected. These were placed in covered glass dishes on moist loam and sand combined in a 1:1 ratio. The dishes were kept at 20–25°C and exposed to 12 hr of fluorescent light/day (400 $\mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$). Germination was monitored daily for five days.

RESULTS

Size and reproductive activity. Differences were apparent between the two study sites in the relationship of reproductive activity to size (Fig. 2, Table 2). The shortest individuals sampled that bore flowers or fruits were 0.99 m tall in the Twin Peaks site and 1.32 m tall in the Ajo Mountain site. In the Twin Peaks site, only three of 14 plants that flowered and were less than 1.49 m in height failed to produce fruits, whereas in the Ajo Mountain site, two of the four reproductively active individuals in the same size range failed to fruit. Despite the greater minimum height of reproductive activity in the Ajo Mountain site, the threshold height above which all plants

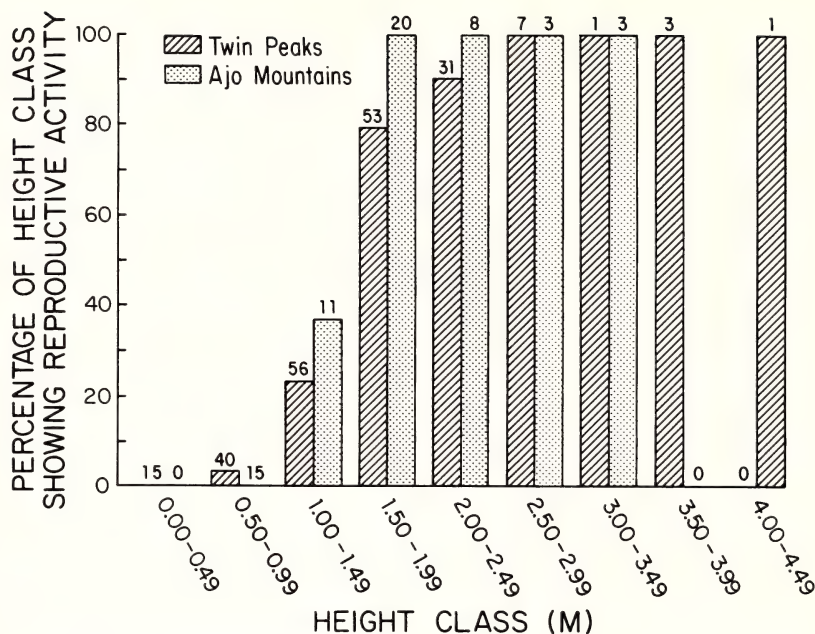


FIG. 2. The percentage of each height class showing evidence of reproductive activity of *Stenocereus thurberi* in the two study plots. Numbers above the bars indicate sample size for each height class.

in that sample produced flowers or fruits was lower (1.50 m) than in the Twin Peaks sample (2.50 m). Similarly, in the Ajo Mountain sample, all plants with more than seven arms produced flowers and fruits (Table 2) during the year of study, whereas in the Twin Peaks sample several plants with more than 10 arms did not flower. Three of the individuals in the Twin Peaks site greater than 2 m tall and with at least seven arms bore flowers, but not fruits. Despite these differences between the two samples, the overall relationship of size to reproductive activity suggests that most individuals of *S. thurberi* begin reproductive growth by the time they are 2–2.5 m tall. By this time, most plants have 4–10 arms.

Seed production per fruit and germinability. Fruits of *S. thurberi* are spherical in shape (Fig. 3, Table 3). The mean weight of the ripe fruits collected was 73.03 g. The significant intercorrelation ($p < 0.001$; Table 4) between fruit dimensions and weight indicates that these characteristics all vary proportionally. On average, seeds accounted for only 3.76 g of the total fruit weight. The mean number of seeds per fruit was 1969, and larger fruits generally produced more seeds than smaller fruits (Table 4). The mean seed weight per

TABLE 2. RELATIONSHIP OF REPRODUCTIVE STATUS TO ARM NUMBER IN *S. thurberi* AT TWO SITES IN ORGAN PIPE CACTUS NATIONAL MONUMENT. Reproducing plants include individuals bearing buds, flowers, or fruits. RP = the number of reproducing plants; n = the sample size for each arm-number category.

Number of arms	Twin Peaks (N = 207)		Ajo Mountains (N = 60)		Total (N = 267)	
	Reproducing plants		Reproducing plants		Reproducing plants	
	RP/n	%	RP/n	%	RP/n	%
1	0/11	(0.0)	—	—	0/11	(0.0)
2	0/19	(0.0)	1/5	(20.0)	1/24	(4.2)
3	1/27	(3.7)	0/5	(0.0)	1/32	(3.1)
4	6/23	(26.1)	6/14	(42.9)	12/37	(32.4)
5	7/16	(43.7)	4/5	(80.0)	11/21	(52.4)
6	13/24	(54.2)	2/5	(40.0)	15/29	(51.7)
7	10/16	(62.5)	5/6	(83.3)	15/22	(68.2)
8	7/10	(70.0)	3/3	(100.0)	10/13	(76.9)
9	9/15	(60.0)	5/5	(100.0)	14/20	(70.0)
10	10/10	(100.0)	4/4	(100.0)	14/14	(100.0)
>10	33/36	(91.7)	8/8	(100.0)	41/44	(93.2)

fruit was not correlated significantly with any of the other fruit characteristics measured (Table 4). Eighty-eight percent of the *S. thurberi* seeds planted had germinated after five days.

DISCUSSION

Reproductive characteristics. In Saguaro National Monument, located approximately 150 km east of OPCNM, Steenbergh and Lowe (1977) reported a minimum reproductive height for *C. gigantea* similar to that reported here for *S. thurberi*. They found that all individuals greater than 2.5 m tall produced reproductive structures and that the smallest individual that showed evidence of reproductive activity was between 1.5 and 1.99 m tall. Steenbergh and Lowe (1977) concluded that healthy *C. gigantea* individuals typically reach reproductive maturity at a height of 2.2 m, or an age of about 30 yr.

Important differences exist between the two species in the relationship of arm number to reproductive activity. Steenbergh and Lowe (1977) found that individuals of *C. gigantea* begin to develop arms after they reach a height of approximately 4.5 m, or more than twice the size at which they typically begin reproducing. In southern Arizona, *S. thurberi* consists of many relatively narrow stems (ca. 15 cm diameter) that emerge from the base of the plant, rather than a primary stem with arms forming several meters above the base. Unlike *C. gigantea*, *S. thurberi* individuals generally do not begin reproducing until after they have more than one arm.

Steenbergh and Lowe (1977) hypothesized that the production of

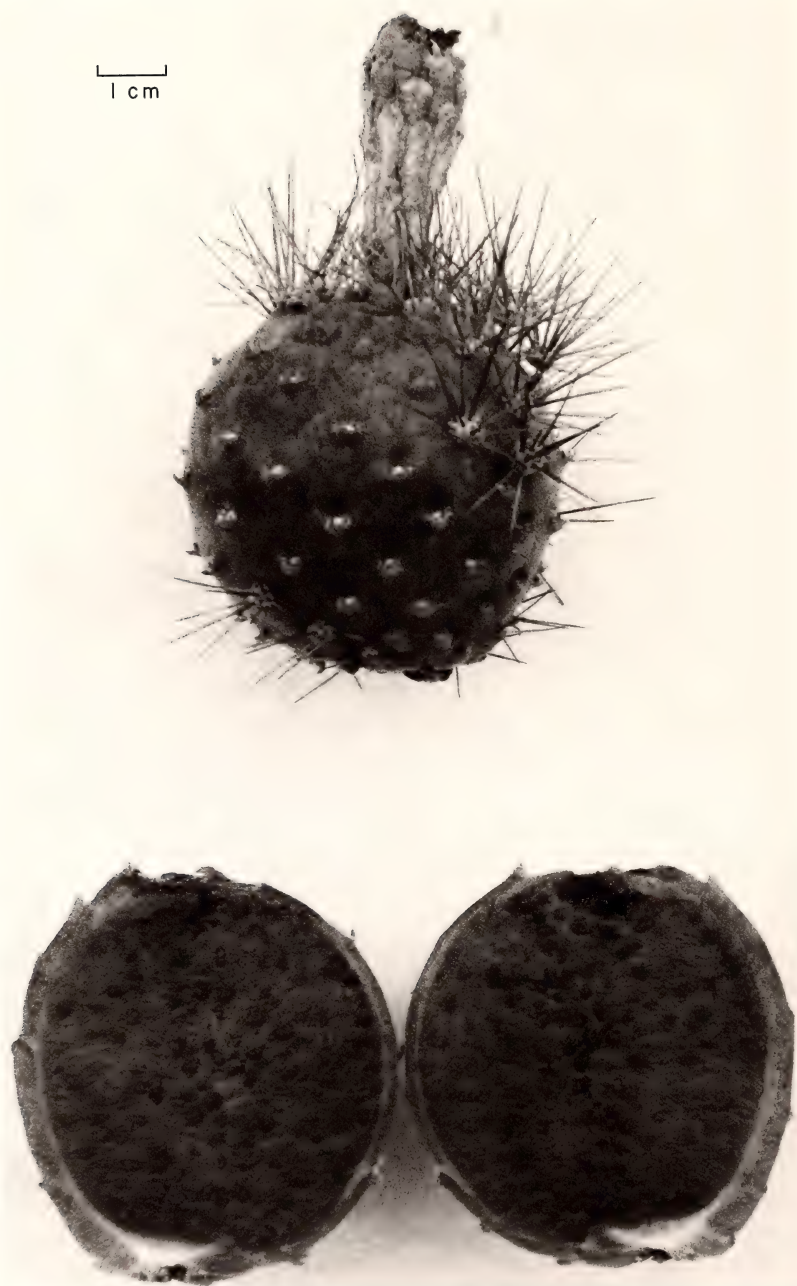


FIG. 3. Fruit of *Stenocereus thurberi*.

TABLE 3. DIMENSIONS, WEIGHT, AND SEED NUMBER OF FRUITS OF *Stenocereus thurberi* (n = 19). Whole fruits were measured with spines and desiccated flower parts removed; seeds from each fruit were air dried after removal of pericarp and flesh. The mean weight/seed by fruit for the sample was calculated by averaging the means for each fruit.

Measurement	$\bar{X} \pm \text{s.d.}$	Range
Whole fruits		
Length (mm)	51.1 ± 6.5	41.4–63.3
Diameter (mm)	52.9 ± 4.9	41.7–63.5
Weight (g)	73.03 ± 23.18	32.19–125.22
Seeds per fruit		
Total weight (g)	3.76 ± 1.43	1.63–6.56
Total number	1969 ± 703	688–3373
Weight/seed by fruit (mg)	1.91 ± 0.23	1.47–2.37

arms in *C. gigantea* increases its reproductive potential and that this is their primary function. Undoubtedly, individuals of *S. thurberi* with numerous arms have a greater reproductive potential than those with few arms, because fruits are only borne on the upper portion of the arms. Whether enhancement of reproductive capacity serves as a selective force in arm production by *S. thurberi*, or is simply a fortuitous consequence of a basally-branched form conferred by different selective constraints is debatable.

Steenbergh and Lowe (1977) reported a slightly greater mean seed number per fruit for *C. gigantea* than I obtained for *S. thurberi*, although results of a t-test ($t = 1.51$, $df = 31$) indicate that this difference is not significant ($p < 0.05$; data for *C. gigantea* fruits were taken from Steenbergh and Lowe 1977). The mean seed weight for *S. thurberi* (1.9 mg) is greater than that reported by Steenbergh and Lowe (1977) for *C. gigantea* (1.3 mg), but the absence of a standard deviation value for mean seed weight for *C. gigantea* precluded calculation of the t-statistic to determine whether this difference is statistically significant.

TABLE 4. SPEARMAN CORRELATION COEFFICIENTS (r_s) BETWEEN FRUIT CHARACTERISTICS (n = 19). ** = significant at $p < 0.0001$; * = significant at $p < 0.05$.

	Mean weight/seed	Seed number	Total seed weight	Fruit weight	Fruit diameter
Fruit length	0.04	0.45	0.39	0.86**	0.82**
Fruit diameter	-0.03	0.47*	0.42	0.95**	
Fruit weight	0.11	0.47*	0.42		
Total seed weight	0.10	0.94**			
Seed number	-0.10				

The germination percentage that I found for *S. thurberi* was similar to the 91% germination for this species (at 25°C with 8 hr photoperiods for 6 days) reported by McDonough (1964). Under the same conditions, he found a slightly higher percentage germination (97%) for *C. gigantea*.

Relationships between environment and reproductive activity. The mean number of fruits borne by individuals of *S. thurberi* was not quantified. Many plants observed during the course of data collection, however, bore at least 50 fruits. With a mean of approximately 2000 seeds per fruit, individuals that bear more than 50 fruits produce about 100,000 seeds in a single season. The results of the germination test indicate that a high percentage of the seeds produced by an individual have the potential of germinating if environmental conditions are favorable. Thus, the reproductive potential of even a small population of *S. thurberi* is great. Field germination percentages and the survival of seedlings, however, have not been determined.

In the Twin Peaks site, some large individuals of *S. thurberi* did not reproduce during 1976, and some that flowered failed to set fruit. Flowering and fruiting among large plants were more consistent in the Ajo Mountain site than in the Twin Peaks site. Variation in moisture regimes between the two study sites may be responsible, in part, for the differences in reproductive activity. In a particularly dry year, such as the one preceding the study, the higher rainfall characteristic of the Ajo Mountains may foster consistent reproductive activity of *S. thurberi* occurring there, while reproductive activity is more sporadic in drier parts of the Monument. Although Thackery and Leding (1929) and Steenbergh and Lowe (1977) reported that drought had little influence on fruit production in the closely related *C. gigantea*, Thackery and Leding (1929) suggested that reproductive activity in *S. thurberi* is more sensitive to drought stress than in *C. gigantea*. Steenbergh and Lowe (1977) also reported that severe freezes may reduce greatly the reproductive activity of *C. gigantea* the following summer. It is unlikely, however, that spatial variation in the occurrence of severe freezes caused the differences in reproductive activity between the two *S. thurberi* sites because of their similar topographic positions (i.e., susceptibility to cold air drainage).

The reproductive traits of *S. thurberi* are well adapted to the variable environment characteristic of the region of study. Near the margin of its range, successful establishment of young individuals of *S. thurberi* is limited by frequent severe freezes (Nobel 1980) and by periodic prolonged drought. Most individuals of *S. thurberi* become reproductively active at heights from 2–2.5 m. The fruiting of very large individuals indicates that plants are reproductively active

throughout most of their adult life. By producing a large quantity of seeds every year for many years, individuals of *S. thurberi* improve the chance that an occasional seed will disperse to a site favorable for germination and growth in a year when climatic factors are favorable, thereby maintaining a stable population.

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REPRODUCTIVE BIOLOGY OF THE TREE
IPOMOEA WOLCOTTIANA (CONVOLVULACEAE)

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ABSTRACT

Ipomoea wolcottiana is an hermaphroditic tree of the tropical deciduous forest of México. It flowers after leaf drop, but may be highly asynchronous among trees if interrupted by rainfall early in the dry season. Anthesis is nocturnal and nectar secretion is constant until after midday. Insect visitors include sphingid moths and 21 species of bees; few of these have characteristics of effective cross-pollinators. The fragrant flowers present abundant pollen, but the sucrose-rich nectar differs between trees by as much as a factor of three. Significant individual variation also occurs in stamen and style length, and flower weight, but only the latter two are correlated. Pollination experiments show self-incompatibility and some female-sterile trees; the latter result is supported by records of up to four years from marked trees, and is unrelated to floral morphology or nectar volume.

Variation between individuals in female fecundity is conspicuous in some species of *Ipomoea*, but the causes have proven difficult to unravel (Martin 1970, Stucky and Beckmann 1982). Although *Ipomoea* is principally a genus of vines, a few species are trees (Lujan 1974, McPherson 1982), a life form that differs substantially from vines in the pattern of breeding systems (Bullock 1985). Tree species of *Ipomoea* are of broader ecological interest because they are common pioneers in the seasonally arid tropics of México, and may have an important role in supporting bee populations in a season when few other trees are in flower ("keystone mutualists" of Gilbert 1980). In this study, we outline the reproductive biology of *I. wolcottiana* Rose, including phenology, nectar production and quality, flower visitors, morphological variation in the flowers, compatibility, and sterility.

STUDY AREA

The present study was carried out from 1980–1987 in lowland Jalisco, México, at the Estación de Biología Chamela (19°30'N,

105°03'W). The summer rainy season lasts about four months, but rains between November and early February account for 11% of the average annual precipitation, with a range of 0–30%; no measurable rain has been recorded from March through late May (Bullock 1986). The vegetation is tropical deciduous forest (Rzedowski 1978, Lott et al. 1987). The flora of the field station includes 20 species of *Ipomoea* (Lott 1985). *Ipomoea wolcottiana* is here a tree of 2–9 m or more, and is scarce except in large areas of disturbance.

MATERIALS AND METHODS

Measurements were made of 10 flowers from each of 17 trees, including length of the style (from the base of the free filament), and of the longest and shortest stamen filaments, and flower weight. Nectar volume was measured on various dates from flowers on 16 trees, with five flowers sampled per tree per hour (at 2330, 0300, 0600, 0900, and 1330 hr local time), although not all trees were collected at all hours. Nectar analyses were made for six trees and included methods described previously for sugars and amino acids (Baker and Baker 1975, Baker and Baker 1982), as well as screening for alkaloids (Dragendorff test), proteins (brom-phenol blue test), and phenolics (p-nitro aniline test). Sugar concentration was measured from nectar spotted on filter paper.

Activity periods of bees were recorded for hourly periods on five days in February and March 1985. The species were rated for abundance and behavioral observations were made, which complemented collections and observations made yearly since 1980. Bee sizes were measured as the width of the scutum at the tegula, for five females of each species (males in three species, see below). Additional observations were made to detect visits by bats and moths, and birds were noted during the day.

Compatibility tests followed the protocol of Bullock (1985), with a total of 17 trees tested in 1982 and 1983. Fruit set was zero on some of these trees, so a sample was marked for yearly observation of fruiting (24 trees in 1982, 36 in 1983–1985). A qualitative rating system with four levels (0–3) was used to accommodate the range of variation of several orders of magnitude and the differences due to canopy size.

Statistical analyses were one-way ANOVA, Spearman rank correlations (r_s), least-square linear regression (r^2) and analysis of covariance (Killian 1981), the Student-Newman-Keuls procedure, and the Mann-Whitney test (Zar 1974). Significance was accepted at the 0.05 level. Plant and animal specimens were deposited in the station's museum or at the Instituto de Biología, U.N.A.M., in México City.

RESULTS

Phenology. The trees flowered in the early months of the dry season, and most were leafless then. In April 1980, the population contained trees with only flowers or fruits, and a few individuals with both. This late and asynchronous reproduction may have been due to rain in late January and early February (46 mm). In 1981, following mid-January precipitation (124 mm), a similar phenology was noted. With no rain from November 1981 through May 1982, flowering occurred in January and February 1982. Leaf fall was well advanced in November 1982, but heavy rains in late November and December (160 mm) caused a major leaf flush (sudden, vigorous growth). Flowering throughout the population was delayed until late February to early March 1983. The next dry season began in November 1983, and flowering followed in January and February, with rain in mid-January (38 mm) causing only a minor flush. The 1984–1985 dry season started in October, but rain in mid-December (85 mm) and in mid-January (19 mm) delayed flowering. In 1986, flowering was very sparse and fruit production zero, presumably due to lack of rain in summer 1985 (60% of previous normal). The next flowering season began in December 1986, and was not interrupted by mid-January rain (25 mm). Near the station buildings, well-watered trees retained some leaves year round, whereas unirrigated trees nearby lost all their leaves in the dry season.

Anthesis. The corolla was furled in bud, and opened gradually after midnight, until the distal half of the corolla was flared perpendicular to the floral axis. The entrance to the effective corolla tube was about 11–12 mm in diameter (Fig. 1). At anthesis, the anthers were dehiscent and nectar was present. The flowers closed permanently the following afternoon.

Nectar. Nectar accumulated throughout the night and morning until at least 1300 hr. The volume-time regressions were all significant and ranged from $r^2 = 0.41$ – 0.94 . Rates of accumulation were heterogeneous (analysis of covariance, $F = 41$), varying from 0.90 – $1.98 \mu\text{l/hr}$. The estimated volume prior to anthesis (2300 hr) differed more than flow rates between trees, ranging from 0.6 – $16.2 \mu\text{l}$. Because the nectar accumulation curves were not heterogeneous in form, the trees can be compared most simply by the volume at a particular hour. At 0900 hr, somewhat after the peak of pollinator activity, accumulated volumes ranged from 11 – $34 \mu\text{l}$ (Table 1). The variation was nearly continuous, with no significant differences between trees differing in rank by less than three (SNK test). No significant trend emerged in relating flower weight to nectar volume ($r_s = 0.51$, Table 1). No significant correlations were found between nectar volume and length of style or stamen ($r_s = -0.09$, -0.10 , respectively). Furthermore, nectar production was not clearly related

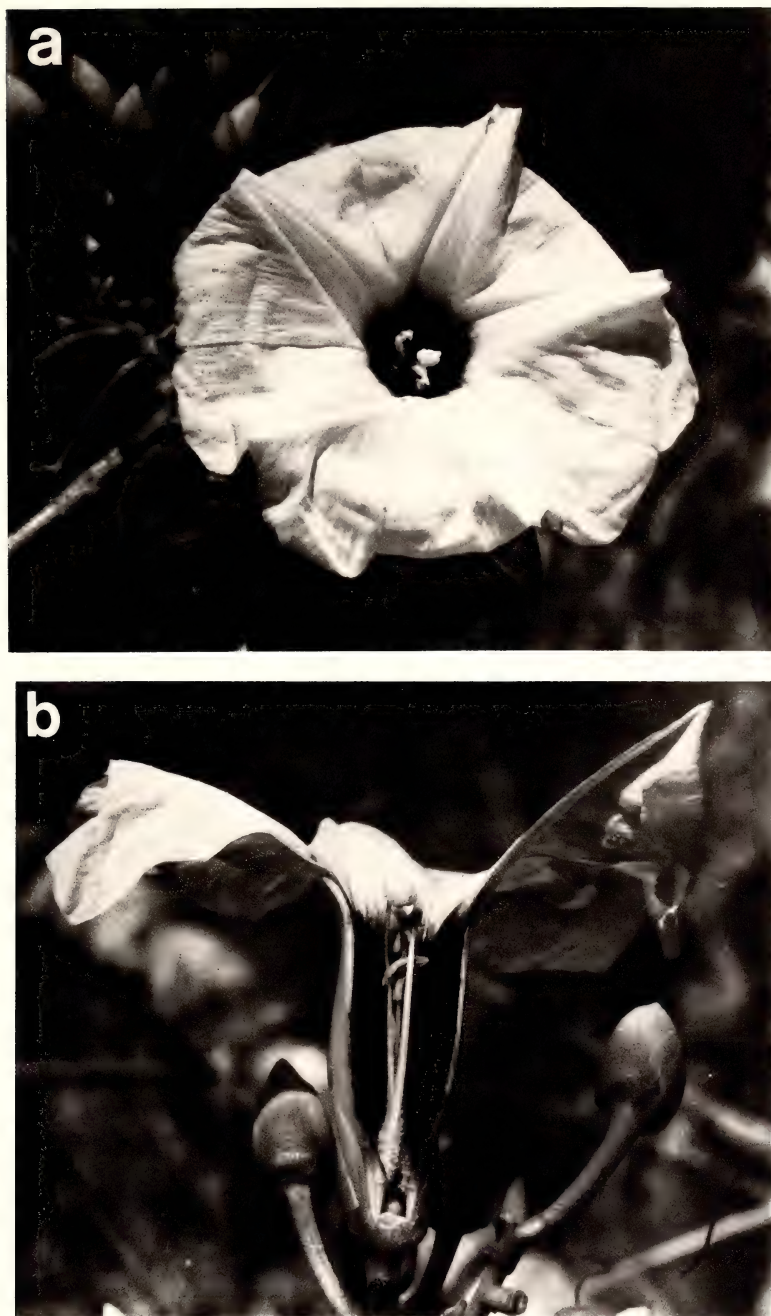


FIG. 1. Flower of *Ipomoea wolcottiana* in nearly axial (a) and cross-sectional (b) views (in situ, unfiltered daylight).

TABLE 1. FLORAL CHARACTERISTICS AND FRUIT SET FROM HAND POLLINATION IN *Ipomoea wolcottiana*. For morphology and nectar volume, the mean and standard deviation are given. Fruit set is given as the proportion (p) of the number of treated flowers (n).

Tree no.	Flower dry weight (mg)	Longest filament length (mm)	Style length (mm)	Nectar volume (μ l)	Fruit from hand pollination			
					Cross		Self	
					p	(n)	p	(n)
5	15.5 \pm 1.0	24.7 \pm 1.8	27.5 \pm 1.5	26.3 \pm 4.1	0.00	(9)	0.00	(17)
11	13.2 \pm 1.1	26.1 \pm 0.7	27.7 \pm 0.9	13.3 \pm 2.3	0.40	(10)	0.00	(17)
15	14.7 \pm 0.8	23.6 \pm 7.0	25.4 \pm 1.0	31.8 \pm 2.9	0.07	(15)	0.00	(17)
20	13.2 \pm 1.0	21.9 \pm 0.7	23.3 \pm 1.3	26.0 \pm 5.3	0.00	(6)	0.00	(12)
21	12.5 \pm 0.4	24.8 \pm 0.9	23.6 \pm 1.2	19.2 \pm 4.1	0.00	(11)	0.00	(11)
25	13.0 \pm 1.1	25.6 \pm 1.1	25.1 \pm 0.7	20.6 \pm 4.7	0.57	(14)	0.00	(19)
26	16.1 \pm 1.4	25.9 \pm 0.6	27.8 \pm 1.0	26.6 \pm 4.2	0.08	(26)	0.00	(25)
27	14.8 \pm 0.4	25.5 \pm 0.8	23.7 \pm 1.5	30.5 \pm 3.2	0.00	(16)	0.00	(17)
28	12.0 \pm 1.5	25.3 \pm 1.2	27.4 \pm 1.0	— —	0.00	(20)	0.00	(20)
29	14.3 \pm 1.4	25.7 \pm 1.2	28.4 \pm 1.2	25.1 \pm 3.0	0.04	(23)	0.06	(32)
30	13.4 \pm 0.8	27.9 \pm 1.3	24.1 \pm 1.0	13.4 \pm 1.4	0.56	(18)	0.00	(21)
31	14.8 \pm 1.0	28.9 \pm 0.7	31.1 \pm 1.3	23.0 \pm 3.1	0.00	(20)	0.00	(26)
32	14.4 \pm 0.6	26.4 \pm 0.5	29.0 \pm 0.9	15.8 \pm 1.4	0.24	(29)	0.00	(27)
33	15.8 \pm 0.6	23.7 \pm 1.2	28.8 \pm 1.3	13.9 \pm 5.0	0.00	(39)	0.00	(30)
34	13.4 \pm 1.0	29.9 \pm 0.9	26.2 \pm 0.8	34.3 \pm 4.5	0.18	(22)	0.00	(34)
35	17.0 \pm 0.4	24.3 \pm 1.2	27.9 \pm 1.3	14.0 \pm 3.6	0.42	(19)	0.00	(40)
36	13.0 \pm 1.9	24.1 \pm 1.4	27.4 \pm 1.1	11.1 \pm 5.2	0.33	(24)	0.00	(23)

to fruit production from hand cross-pollination ($r_s = -0.20$). The volume in trees that are fertile by hand cross-pollination was not different from that of sterile trees (Mann-Whitney test).

Amino acid concentration in the nectar was low (1–2 on the histidine scale). The sugar component was mostly sucrose, with ratios of sucrose to glucose plus fructose ranging from 2.0–3.4 ($\bar{X} = 2.42$). Sugar concentration was measured for four trees, giving the following values: 25.8% (w/w), 29.6%, 27.7%, and 38.8%. None of the samples showed detectable traces of alkaloids or proteins, but the reaction for phenolics varied from not detectable to moderately strong. The flowers also had a strong fragrance. Apparently glandular hairs were present on the lower part of the filaments, but secretions have not been obtained in analyzable quantity.

Flower visitors. Twenty-one species of bees were found feeding at the flowers, but nine of these were rare (Table 2). Most of the species were represented by females or workers, but only males were noted for *Eulaema polychroma*, *Melissodes tepaneca*, and *Melitoma marginella*. The activity of the nocturnal *Megalopta* sp. remained poorly defined due to their reaction to light. *Ceratina capitosa* spent much time inactive inside the flowers, but this behavior may be limited to males. The range of body widths was almost an order of magnitude (Table 2) and included the largest and smallest bees in the Chamela fauna. The larger species always brushed against the anthers, and usually the stigma, on entering. All bee species foraged for nectar by entering the corolla tube. All species can become dusted by fallen pollen in the corolla tube, but only six species were noted as pollen collectors, including four of the common species (Table 2).

Other diurnal visitors included *Cacicus melanicterus* (Bonaparte) (Aves: Icteridae) and *Amazilia rutila* (DeLattre) (Aves: Trochilidae). Nocturnal observations showed some visitation by *Erinnyis* sp. (Lepidoptera: Sphingidae) and we have identified pollen collected from *E. ello* (L.) as *I. wolcottiana*. No visits by bats have been observed.

Style and stamen length. The length of the style and longest stamen varied significantly between trees (Table 1; ANOVA, $F = 39$ and 35 , respectively). The length of styles but not of stamens was correlated with flower weight (respectively, $r_s = 0.52$, $p < 0.05$; $r_s = -0.02$). Stamen and style lengths were not significantly correlated ($r_s = 0.28$), but showed similar ranges of variation, 8.0 and 7.8 mm, respectively. Mean length of the shortest stamen varied significantly ($F = 21$, range 16.5–24.8 mm) and correlated with length of the longest stamen ($r_s = 0.58$).

Compatibility and sterility. Of those trees that bore any fruit as a result of pollination by hand, all except one were self-incompatible (Table 1). Because all hand pollination was done between 0630 hr

TABLE 2. BEE VISITORS TO FLOWERS OF *Ipomoea wolcottiana*. Size is scutum width in mm for females, or males (*). Activity period is time of day by hour intervals (n.d. = species not observed in 1985). Notes are given for species observed collecting pollen (p), and for those more than rare in abundance.

Family and species	Size	Activity period and notes
HALICTIDAE		
<i>Augochlora smaragdina</i> Friese	1.9	9-13
<i>Augochlora albiceps</i> Friese	2.0	10-12 (p)
<i>Augochlora nigrocyanea</i> Cockerell	2.1	8-16 (p, few)
<i>Megalopta</i> sp	2.6	?0-7 (? , common)
ANTHOPHORIDAE		
<i>Ceratina capitosa</i> F. Sm.	2.4	8-17
<i>Ceratina</i> sp 1	1.2	10-17
<i>Ceratina</i> sp 2	1.0	10-14
<i>Centris nitida</i> F. Sm.	4.6	n.d.
<i>Centris segregata</i> Crawford	5.4	n.d.
<i>Melissodes tepaneca</i> Cresson	2.7*	9-15 (common)
<i>Melitoma marginella</i> (Cresson)	3.1*	8-15 (common)
<i>Xylocopa fimbriata</i> Fabricius	8.8	10-11
<i>Xylocopa mexicanorum</i> F. Sm.	6.9	6-12 (p, common)
<i>Xylocopa muscaria</i> (Fabricius)	5.2	11-12
<i>Xylocopa t. tabaniformis</i> (F. Sm.)	5.8	6-10 (p, common)
APIDAE		
<i>Eulaema polychroma</i> (Mocsary)	6.4*	10-11
<i>Melipona beecheii</i> Bennett	3.3	6-11 (few)
<i>Trigona buyssoni</i> Friese	0.9	9-13 (few)
<i>Trigona fulviventris</i> Guerin	1.6	8-12 (few)
<i>Trigona hellwegeri</i> Friese	1.8	n.d. (few)
<i>Trigona orizabaensis</i> Strand	1.7	6-17 (p, common)

and 1300 hr, there was no evidence for the breakdown of incompatibility barriers with flower age. No fruit were produced from hand pollination on seven of 17 trees tested, and 10 of 17 had fruit set of 10% or less. Fruit set was not significantly correlated with either style or stamen length or flower weight (Table 1; respectively, $r_s = 0.03, 0.31$, and -0.09).

The exceptionally low fertility of *I. wolcottiana* compared with other tree species at Chamela (Bullock 1985) led to further observations in the population at large. Some trees of *I. wolcottiana* produced massive numbers of flowers, but produced few fruits or were completely barren, whereas adjacent trees, sometimes with interlaced canopies, produced many fruits. The differences between fruit production in trees with low and high fecundity were consistent. Data from four consecutive years showed no tendency to oscillate between barren and productive states, and the majority of trees of low or moderate average fecundity had no peak year (Table 3).

TABLE 3. MAXIMUM FRUIT PRODUCTION AND FREQUENCY OF (FRUIT-)BARREN YEARS FOR INDIVIDUALS OF *Ipomoea wolcottiana* WITH DIFFERENT AVERAGE FRUIT PRODUCTION.

Individual mean fruit production 1982 (or 83)– 1985	n	Percent of trees attaining a given maximum level of fruiting				Overall frequency (%) of tree-years with no fruit
		0	1	2	3	
0–0.49	8	88	12	0	0	97
0.50–1.39	8	—	62	38	0	10
1.40–2.19	7	—	—	57	43	0
2.20–3.0	13	—	—	—	100	4

DISCUSSION

The annual phenology of *I. wolcottiana* varies considerably and apparently is conditioned by the timing of rainfall. Thus, flowering may begin in early December or not until late February, or may split between early and late starting trees, and some individuals may flower twice in one season. Drought appears necessary for the onset of flowering, but rains in December or January can cause flushing in trees not well advanced in flower development. Desynchronized or delayed flowering has occurred in four years from 1980–1987. On a local spatial scale, soil and vegetation conditions affect the timing of drought experienced by the trees, which probably increases asynchrony in the population. Whatever the result for plant fitness, asynchronous and delayed flowering may benefit flower visitors by prolonging the availability of nectar. Also, the prolonged presence of immature fruit may benefit pre-dispersal seed predators (Schlising 1980, Augspurger 1981), which include *Megacerus cubicus* (Motschulsky) (Bruchidae), and unidentified species of Curculionidae, Diptera, and Lepidoptera. Other trees flowering during the dry season at Chamela are largely unresponsive to rain in those months.

The population is not limited to pollination by either nocturnal or diurnal animals. Nectar flow continues from late night anthesis to midday wilting. Also, the sugar and amino acid analyses are consistent with those from many species pollinated by sphingid moths or large bees (Baker and Baker 1982). Despite the observed diversity of visitors, most of the bees do not reliably contact the anthers or stigma on account of body size or behavior. Altogether, they must remove considerable nectar. *Xylocopa mexicanorum* and *X. tabaniformis* are the only bee species that pollinate *I. wolcottiana* consistently, are common, and move frequently between trees. *Ceratina capitosa* also might be a significant pollinator, as are its congeners on flowers of other *Ipomoea* species. Moreover, the importance of

nocturnal visitors remains to be clarified, especially for Sphingidae and *Megalopta*. Bats were not observed visiting *I. wolcottiana*, and the nectar sugar composition is contradictory to the trend in species pollinated by microchiroptera (Baker and Baker 1982). However, abundant pollen of *Ipomoea* sp. was found in stomachs of the bats *Leptonycteris yerbabuenae* Martínez and Villa and *Glossophaga soricina* Pallas in Guerrero (Quiroz et al. 1986).

Nectar quantity differs among individuals, but we presently have no reason to interpret variation around the linear regressions of quantity on time as representing time-varying secretion rate. The latter has been shown for a few trees and was suggested as a mechanism to induce cross-pollination (Frankie and Haber 1983).

Variation within and between individuals in style and stamen length has been reported in few *Ipomoea* species (Wilson 1977, Ennos 1981) despite many studies of pollination. In *I. wolcottiana*, the difference between longest and shortest stamens is always substantial (3–8.2 mm), although its distribution was not normal or unimodal. Greater anther-stigma distance entailed an order of magnitude greater outcrossing frequency in *I. purpurea* compared with *I. hederacea* (Ennos 1981). Also, seed set from autogamy in *I. purpurea* was negatively correlated with anther-stigma distance (Ennos 1981). The style-filament difference in *I. wolcottiana* ranged from –3.8 to 5.1 mm, but was not normal or unimodal, and was not different between trees that were fertile or barren in hand cross-pollination (Mann-Whitney test).

Thus, *Ipomoea wolcottiana* varies significantly in morphological and functional characters that are not sorted into well-defined groups or correlated in interpretable patterns. If the system is evolving, the path is unclear as yet. As a further element in the breeding system, variation in male fertility has not yet been detected. A limited search for male sterility, using cotton blue in lactophenol (in vitro germination of *Ipomoea* pollen is problematic; Martin and Ortiz 1966, Stucky and Beckmann 1982), did not show any notable differences among trees. A similar condition was described for *Mirabilis froebelii* (Behr) Greene (Nyctaginaceae; Baker 1964), where variability in the floral organs had no apparent relationship to the breeding system.

In fruit production, most variation was among trees of intermediate to low average fecundity, and non-fruiting trees were consistently barren. Thus, this *I. wolcottiana* population does not consist of individuals that fruit heavily on a supra-annual basis with intervening years of little or no fruit (Janzen 1978). The proportion of trees with different bearing levels is unknown, because the sample population was not taken at random. Barrenness might be due to nutrient limitation, lack of pollination, lack of compatible pollen, genetic sterility, or cytogenetic problems. The former two alternatives are not probable because trees with different levels of fecundity

(by natural or hand pollination) were frequently commingled. The consistent fruiting behavior or barrenness and the failure of pollination by hand to overcome barrenness of some trees lead us to conclude that some form(s) of female sterility exists in this population. As noted above, this is not correlated with a suite of floral characters. Female sterility is known in other *Ipomoea* species (Martin and Cabanillas 1966, Stucky and Beckmann 1982). Chromosomal aberrations and imbalance add to the problems in *I. batatas* (L.) Lam. (Ting et al. 1957). Thus, the sterility problem may require cytological study.

Female fecundity of some vine species is limited by the scarcity of compatible mates (Martin 1968, Stucky and Beckmann 1982). The potential for incompatible pollination is suggested by the results of extensive tests with the diploid *I. setifera* Poir., which revealed 10 incompatibility groups (Martin 1968). In vines, extensive clonal growth (Peñalosa 1984) or establishment from vegetative fragments may result in patches containing one or very few incompatibility groups. When plants establish only from seed, as in *I. wolcottiana*, lack of compatible mates seems unlikely to account for a wide range of fecundities. However, when trees are partially or completely self-incompatible, such a situation may arise. For example, in some sparse populations of *Inga* species (Mimosoideae) fruit set was limited by the low frequency of more distant and more successful crosses (Koptur 1984). The effects of population structure and its variation in the disturbance-following *I. wolcottiana* remain to be assessed in relation to both the generalized and individually variable characters of the breeding system we have described.

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ALPINE ANNUAL PLANT SPECIES IN THE WHITE MOUNTAINS OF EASTERN CALIFORNIA

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ABSTRACT

The White Mountains resemble the Sierra Nevada in having an unusually high concentration of alpine annual plant species. Thirteen species of annuals comprise 8% of the alpine flora of the White Mountains. Most species (69%) have distributions that extend throughout western North America; however, they are known to occur above treeline only in the White Mountains and Sierra Nevada. Two of 13 species of alpine annuals in the White Mountains have distributions from near sea level to the alpine, three occur from the desert to the alpine, and seven have distributions from the coniferous forest to the alpine in California. Three additional species (*Che-nopodium rubrum*, *Gentiana tenella*, and *G. prostrata*), generally known as annuals, function as biennials in alpine habitats of the White Mountains.

Few species of annual plants occur in alpine environments (Billings and Mooney 1968, Bliss 1971, Billings 1974). This probably reflects the inability of most annuals to successfully complete their life cycle in a short, cold growing season. The Sierra Nevada of California, however, has an unusually large number of annual plants at high elevations. Sharsmith (1940), for example, lists about 10 annuals in the alpine zone, and Went (1953) and Jackson (1985) describe approximately 47 annuals in the high subalpine and alpine zones.

The ability of annuals to occupy alpine habitats in the Sierra Nevada may be caused by relatively high levels of solar radiation and more moderate conditions (due to fewer summer storms) than are generally found in other alpine areas (Chabot and Billings 1972, Jackson 1985). An abundance of annual plant species at lower elevations, some of which may have been pre-adapted to conditions at higher elevations, contribute to the increased number of alpine annuals in the Sierra Nevada (Went 1953, Chabot and Billings 1972, Jackson 1985).

The alpine zone of the White Mountains is similar to the Sierra Nevada in having relatively warm dry summers with high levels of solar radiation and large numbers of annuals at lower elevations (Lloyd and Mitchell 1973, Major and Taylor 1977). On this basis,

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a relatively high concentration of annuals should occur at high elevations in the White Mountains. This study tests this prediction and provides information on the distribution of alpine annual plant species in the White Mountains of eastern California.

STUDY AREA

The White Mountains are located in the eastern part of central California (37°13'–38°N and 117°55'–118°25'W), with the extreme northeastern portion extending into Nevada. The range is approximately 90 km long and 32 km wide at its widest point and is about 2278 km² in area. Because the Sierra Nevada occurs immediately to the west, the White Mountains are in a pronounced rain shadow and the vegetation is Great Basin in character (Lloyd and Mitchell 1973, Major and Taylor 1977). The four main plant zones described in Lloyd and Mitchell (1973) are desert scrub (1220–1980 m), pinyon woodland (1980–2895 m), subalpine forest (2895–3505 m), and alpine tundra (3505–4340 m). Within these vegetation zones, they list 811 taxa of vascular plants of which 20% (160 species) occur in the alpine zone. Recent collections have increased the total number of known species in the White Mountains to 988 (Morefield 1986).

Climatic records from 1953 through 1973 at the Barcroft Laboratory (elevation 3801 m) of the White Mountain Research Station indicate a mean July temperature of 7.4°C, a mean January temperature of –9.1°C, a mean annual temperature of –5.8°C, and a mean annual precipitation of 49.6 cm, of which 18.3% (9.1 cm) falls during June, July, and August (Pace et al. 1974).

METHODS

The number and proportion of annual plant species in each of the four major plant zones of the White Mountains were based on species distributions given in Lloyd and Mitchell (1973). Life cycles for species not included in this flora were obtained from other floras (primarily Munz 1968, Hitchcock et al. 1969). Geographic affinities were categorized as cosmopolitan, western North American (widely distributed at low and high elevations from the Pacific Coast to the Rocky Mountains), and endemic (restricted to the White Mountains and nearby Sierra Nevada and Sweetwater ranges) according to descriptions in Munz (1968), Hitchcock et al. (1969), and Jackson (1985). Elevational distributions were based on Lloyd and Mitchell (1973) and Spira (pers. obs.) for the White Mountains and Munz (1968) for California. Field observations by the author were confined to the southern part of the range (south of White Mountain Peak).

Voucher specimens were deposited at JEPS. Nomenclature follows Lloyd and Mitchell (1973); for species not included in this source, nomenclature follows Munz (1968).

RESULTS AND DISCUSSION

The number and proportion of annual plant species in each of the major plant zones of the White Mountains are shown in Fig. 1. Annuals become progressively less common with increasing elevation. For example, an analysis of species distributions as listed in Lloyd and Mitchell (1973) indicates that the desert scrub (the lowest zone) has 148 annuals (comprising 35% of the desert flora), whereas the alpine zone has only five annuals (comprising 3% of the alpine flora).

Field observations by the author from 1980–1985 revealed eight additional annuals in the alpine zone (Table 1). This increases the known number of alpine annuals to 13 species (8% of the alpine flora) in the White Mountains. Because annuals are easily overlooked due to their small size and short life cycle, further field studies would undoubtedly reveal additional species in each plant zone. Although the data shown in Fig. 1 underestimate the total number of annual plant species, they do indicate the relative number of annuals in each of the four major plant zones.

The 13 species of alpine annuals in the White Mountains represent 11 genera in 10 families (Table 1). This list is conservative in that it does not include species having an annual and/or biennial life cycle (discussed later) or species described as annuals to perennials (e.g., *Calyptridium umbellatum* var. *caudiferum*, *Androsace septentrionalis* ssp. *subumbellata*). Also, because my field observations were limited to alpine areas in the southern part of the range (south of White Mountain Peak), additional alpine annuals may occur in the northern part of the range.

Geographical distribution. Alpine annuals in the White Mountains generally have wide geographical distributions (Table 1). Nine of 13 species (69%) have a western North American distribution, two (15%) are weedy annuals with a cosmopolitan distribution, and only two species (15%) are endemic to the White Mountains and nearby Sierra Nevada-Sweetwater ranges.

None of the nine alpine annuals with a western North American distribution are known to occur in the alpine zone outside of the White Mountains and Sierra Nevada. The apparent ability of these nine species to occur at higher elevations in the White Mountains and Sierra Nevada relative to other mountain ranges could be explained by a warmer, drier growing season. In lower radiant energy areas, there may not be sufficient time for annuals to complete their life cycle and form viable seed, particularly in unusually short growing seasons (Jackson 1985).

Jackson (1985) lists the proportion of annuals at or above treeline in a number of western North American mountain ranges. Of the 19 areas sampled, seven (37%) had less than 1% annuals, nine (47%)

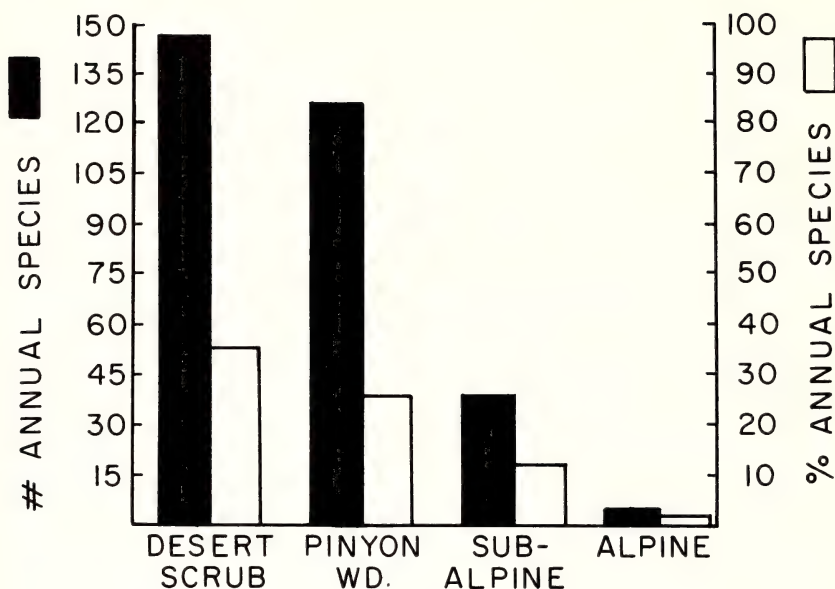


FIG. 1. Number of annual plant species and percent annuals within four main plant zones of the White Mountains based on Lloyd and Mitchell (1973). Recent field observations by author have increased the known number of alpine annuals in the White Mountains from 5 to 13 species (8% of alpine flora).

had 1–4% annuals, and only three (16%) had more than 4% annuals at or above treeline. The Wassuk Range, NV (4.3% annuals), Charleston Mountains, NV (7.6% annuals), and Hall Natural Area, Sierra Nevada, CA (8.3% annuals) comprise the latter group. The Wassuk Range and Charleston Mountains were based on samples of only 70 and 39 species, respectively. Consequently, more comprehensive surveys need to be made prior to evaluating these two areas.

The proportion of annuals in the alpine flora of the White Mountains was comparable to the Hall Natural Area of the Sierra Nevada, the area with the highest proportion of alpine annuals in Jackson's (1985) survey of western North American mountain ranges. Although annuals comprised about 8% of the alpine flora in both ranges, the number of alpine annuals in the Sierra Nevada was much greater than in the White Mountains (47 vs. 13 species). In addition to a larger pool of species, the Sierra Nevada survey included annuals in both the high subalpine and alpine zones (Jackson 1985), whereas only annuals known to occur above treeline were included in the present survey.

TABLE 1. SPECIES, FAMILY, AND GEOGRAPHIC AFFINITY OF ALPINE ANNUAL PLANT SPECIES IN THE WHITE MOUNTAINS. ¹ = Species listed in alpine zone of the White Mountains by Lloyd and Mitchell (1973); ² = Restricted to White Mountains and nearby Sierra Nevada and Sweetwater ranges; ³ = Extends into eastern North America as a weed.

Species	Family	Geographic affinity
<i>Cryptantha glomeriflora</i> ²	Boraginaceae	Endemic
<i>Mimulus coccineus</i> ²	Scrophulariaceae	Endemic
<i>M. suksdorfii</i> ¹	Scrophulariaceae	w. North American
<i>Nama densum</i> ¹	Hydrophyllaceae	w. North American
<i>Juncus bryoides</i>	Juncaceae	w. North American
<i>Gayophytum racemosum</i>	Onagraceae	w. North American
<i>Gymnosteris parvula</i> ¹	Polemoniaceae	w. North American
<i>Eriogonum cernuum</i> ¹	Polygonaceae	w. North American
<i>Calyptridium roseum</i> ¹	Portulacaceae	w. North American
<i>Chenopodium atrovirens</i>	Chenopodiaceae	w. North American
<i>C. leptophyllum</i> ³	Chenopodiaceae	w. North American
<i>Monolepis nuttalliana</i>	Chenopodiaceae	Cosmopolitan
<i>Capsella bursa-pastoris</i>	Brassicaceae	Cosmopolitan

Elevational distribution. Upper elevational extremes for alpine annuals in the White Mountains (Table 2) were consistently higher than those listed by Munz (1968) for California. Because elevational distributions in large floras are not always reliable, it is unclear whether or not alpine annuals in the White Mountains occur at higher elevations than elsewhere in California.

In the White Mountains, however, alpine annuals generally have broad elevational distributions (Table 2). Ten of the 13 species (77%) occur at elevations ranging from less than 1850 m to more than 3500 m. Within California, two of the 13 species (*Capsella bursa-pastoris* and *Monolepis nuttalliana*; 15%) have distributions from near sea level to the alpine, three species (23%) occur from the sagebrush (desert) scrub to the alpine, and seven species (54%) have distributions from the coniferous forest to the alpine (Table 2).

Jackson (1985) found that alpine annuals in the Sierra Nevada also have broad elevational ranges and suggests they migrated to higher elevations from lower elevation populations. Went (1948) and Chabot and Billings (1972) also suggest a low elevation origin for Sierran alpine annuals and note that conditions in the alpine in July and August are similar to those at lower elevations in March and April (e.g., high light levels, large diurnal temperature fluctuations, and limited moisture availability). Consequently, lower elevation annuals may have been pre-adapted, at least to some extent, to an alpine environment.

Axelrod (1981) suggests that a warmer, drier climate in the re-

TABLE 2. PLANT COMMUNITY AND ELEVATIONAL RANGE OF ALPINE ANNUALS IN CALIFORNIA (MUNZ 1968) AND UPPER ELEVATIONAL EXTREME IN WHITE MOUNTAINS (LLOYD AND MITCHELL 1973 AND THIS STUDY). * = J. Morefield, pers. comm. ** = Not available.

Species	Plant community	Elevation (m)		Highest elevation (m) in White Mtns.
		Low	High	
<i>Nama densum</i>	sagebrush scrub to lodgepole forest	910	3570	3570
<i>Calyptidium roseum</i>	sagebrush scrub to lodgepole forest	1520	3200	3750
<i>Chenopodium leptophyllum</i>	sagebrush scrub to yellow pine forest	1520	2440	3750
<i>Chenopodium atrovirens</i>	pinyon juniper wd. to red fir forest	1220	3350	3780
<i>Eriogonum cernuum</i>	**	2130	3050	3200
<i>Juncus bryoides</i>	montane coniferous forest	1280	3350	3660
<i>Gayophytum racemosum</i>	montane coniferous forest	1520	3350	3970*
<i>Mimulus suksdorfii</i>	montane coniferous forest to alpine	1520	3960	4050
<i>Cryptantha glomeriflora</i>	montane coniferous forest	1830	3350	3750
<i>Gymnosotis parvula</i>	bristle-cone pine forest	2530	3600	3830*
<i>Mimulus coccineus</i>	lodgepole pine forest to alpine	2440	3660	3980
<i>Monolepis nuttalliana</i>	many communities	**	2740	3970*
<i>Capsella bursa-pastoris</i>	many communities	**	2130	3540

rothermic (ca. 8000–4000 yr B.P.) facilitated species migrations from lower to higher elevations in the Sierra Nevada (and presumably in the White Mountains). Thus, a number of annuals may have migrated successfully into the alpine zone at this time. As temperatures dropped and rainfall increased following the xerothermic, some annuals probably were eliminated, whereas others may have persisted in favorable microsites at high elevations.

Went (1948) and Chabot and Billings (1972) suggest that nearby deserts were the primary source of alpine annuals in the Sierra Nevada. In a recent floristic study, Jackson (1985) suggests that montane coniferous forests were probably the primary source of alpine annuals in the Sierra Nevada. Because 23% of alpine annuals in the White Mountains extend from the sagebrush (desert) scrub to the alpine and 54% extend from the coniferous forest to the alpine, both the desert and forest were probably important source areas for alpine annuals in the White Mountains.

Habitats. The alpine annuals observed in this study were almost always found on bare soil, and often on dry south-facing slopes. The high light levels, comparatively warm temperatures, and reduced competition for soil moisture in such habitats enhance the ability of annuals to successfully complete their life cycle in a short growing season (Jackson and Bliss 1982).

Alpine annuals were observed frequently along roadsides and grazed areas in the White Mountains, which suggests humans and domestic animals (e.g., sheep and cattle) have increased available habitat and may have introduced seeds of some annuals into the alpine zone. This was probably the case for six weedy annuals restricted to a disturbed roadside area immediately south of the entrance gate to the Barcroft Laboratory, where cars occasionally parked and where horses were tethered during the fall hunting season. Because populations of five of these species (*Sisymbrium irio*, *S. orientale*, *Descurainia sophia*, *Stellaria media*, and *Senecio vulgaris*) were small (generally fewer than 10 plants), highly localized, and present in only one or at most two of the six years (1980–1985) observations were made, they were not included in my list of alpine annuals in the White Mountains.

Capsella bursa-pastoris was a sixth weedy annual restricted to the same roadside area. Unlike the other five species, however, a stable population of 25 to several hundred individuals was maintained during five successive years, and the area occupied by this species increased during the period of study. Thus, *C. bursa-pastoris* appears to have successfully colonized the alpine zone; but it and several other weedy alpine annuals (e.g., *Monolepis nuttalliana*, *Chenopodium atrovirens*, and *C. leptophyllum*) probably would not be present, or would be much less common in the alpine zone of the White Mountains, were it not for the presence of disturbed areas.

Life cycle variation. Except for *Nama densum* and *Eriogonum cernuum*, I observed each of the 13 alpine annuals described here under field conditions. As expected, individuals of each species germinated, flowered, fruited, and died within a single summer. In contrast, several other species, generally described as annuals, exhibited a biennial life cycle in alpine habitats of the White Mountains. For example, *Gentiana tenella* is described as an annual and *G. prostrata* as an annual and/or biennial in regional floras (e.g., Abrams and Ferris 1960, Munz 1968, Hitchcock et al. 1969). In the White Mountains, however, individuals of both species consistently form a vegetative rosette during their first summer, overwinter as a taproot, and then flower, fruit, and senesce during their second summer. Unlike a number of purported biennials in which plant size (rather than age) determines when flowering occurs (Gross 1981), individuals of *G. tenella* and *G. prostrata* flowered in their second year regardless of plant size (Spira 1983).

Chenopodium rubrum is known as an annual that occurs at elevations to 1000 m in Britain, 2000 m in the European Alps, and 3000 m in the United States (Williams 1969). In the White Mountains, however, I have observed *C. rubrum* in alpine habitats to 3750 m, where individuals grow vegetatively one summer and then flower, fruit, and die during their second summer.

A biennial rather than annual life cycle in alpine individuals of *C. rubrum* may be influenced by several factors. First year plants may fail to reach some critical size before flowering can be induced, individuals may require a cold treatment (as overwintering plants would receive) prior to flowering, or individuals may not receive the necessary photoperiod to induce flowering during their first summer's growth (Harper 1977). It would be interesting to know whether the shift in life cycle in *C. rubrum* is a genotypic response (i.e., life cycle ecotypes over an elevational gradient) or an environmentally controlled (phenotypic) response, and at what elevation the shift from an annual to a biennial life cycle occurs.

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PROSOPIS (MIMOSACEAE) IN THE
SAN JOAQUIN VALLEY, CALIFORNIA:
VANISHING RELICT OR RECENT INVADER?

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ABSTRACT

The presence of at least two species of mesquite (*Prosopis glandulosa* and *P. pubescens*) in the San Joaquin Valley of California has been explained previously as the result of the invasion of Mojavean floral elements during the Xerothermal period some 8000–5000 years B.P. I propose that a number of lines of negative evidence argue for the establishment and spread of both species within approximately the last 120 years.

The mesquites (Mimosaceae: *Prosopis*) are a group of woody legumes restricted to the New World. *Prosopis* contains 10 species that range from Argentina and Chile north to the west-central United States. Most species are large shrubs or trees, some of which exceed 12 m. In subtropical regions, *Prosopis* species are often physiognomic dominants or codominants that cover extensive areas.

Two of the four species of mesquite that occur in California are native. *Prosopis pubescens* Benth. (Screwbean or Tornillo) primarily inhabits washes and bajadas in the southern Mojave and Sonoran deserts in California, and ranges widely throughout the southwestern United States and Mexico. *Prosopis glandulosa* L. Benson (Honeybean mesquite) also ranges widely in the southwest and in the deserts of California. It is more widespread than *P. pubescens* in its habitat preferences, however, and occurs in xeric grasslands, on the fringes of lake beds, and in flood plains, washes, and other riparian areas. *Prosopis velutina* Woot. (Velvet mesquite) is native to the Arizona-Sonora region, and also has a scattered distribution in California, which suggests that it is naturalized in this area. Benson (1941) and Munz (1959) have considered *P. velutina* to be a variety of *P. glandulosa*. *Prosopis strombulifera* Lam. (Benth.) is native to South America and is established near Bard, Imperial Co. (Munz 1959).

The first three species noted have disjunct distributions in California, with populations present in the San Joaquin Valley (SJV)

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that are some distance from the main body of their range in the state. In this disjunct area, *P. glandulosa* occurs primarily along the floodplain of the north fork of the Kern River, between Bakersfield and the former bed of Buena Vista Lake. Isolated populations occur throughout the valley and adjacent foothills north to Alameda Co. and east to the Sierra Nevada as far north as Fresno Co. (Fig. 1). Benson (1941) reported an unvouchered occurrence of *P. glandulosa* in the Cuyama River Valley, San Luis Obispo Co. *Prosopis pubescens* is known only from Warthan and Los Gatos canyons in western Fresno Co. and San Emigdio Canyon in southwestern Kern Co. Hilu et al. (1982) reported *P. velutina* from the vicinity of Bakersfield, where it occurs with *P. glandulosa*.

Barbour and Major (1980) concluded that *P. glandulosa* became established in the SJV during the climatic warming trends of the Xerothermal period, between 8000–5000 yr B.P. At this time and during the Pleistocene, elements of the Mojavean biota presumably invaded the Central Valley. Such organisms included *Sceloporus magister* Hallowell (desert spiny lizard), *Xantusia vigilis* Baird (desert night lizard), *Gopherus agassizi* (Cooper) (desert tortoise), *Ephedra viridis* Cov., *E. californica* Wats., and *Yucca whipplei* Torr. As the climate cooled, some species were extirpated (e.g., the desert tortoise), whereas others became restricted to the drier parts of nearby mountains (e.g., the Diablo and Temblor ranges).

A number of lines of evidence, however, indicate that the presence and spread of *P. glandulosa* and *P. pubescens* in the SJV are due to human-induced factors, and that prior to the 1870's neither species existed there. Support for this hypothesis is based largely upon negative evidence, such as a lack of documentation of the extended occurrence of either species where it would be expected to exist. I summarize the salient points in the present paper.

HISTORICAL EVIDENCE

Available historical accounts of expeditions through areas where mesquite now occurs or occurred in the recent past lack documentation of the presence of the species. A particularly interesting account is that of Lt. George Derby, who was commissioned by the War Department in 1850 to survey the "Tulare Valley" (the area between Tulare and Buena Vista lakes) for the purpose of establishing a military outpost. Derby's party traveled along the north bank of the north fork of the Kern River to the north shore of Buena Vista Lake. His account of the area (Boyd 1977) reads as follows: "Like other bodies of water in the valley, it is nearly surrounded by tules [*Scirpus*], and upon its north and east banks there is a heavy growth of willows. A slough, some sixty miles in length [Goose Lake Slough], connects it with the swamps and bodies of standing water in the bed

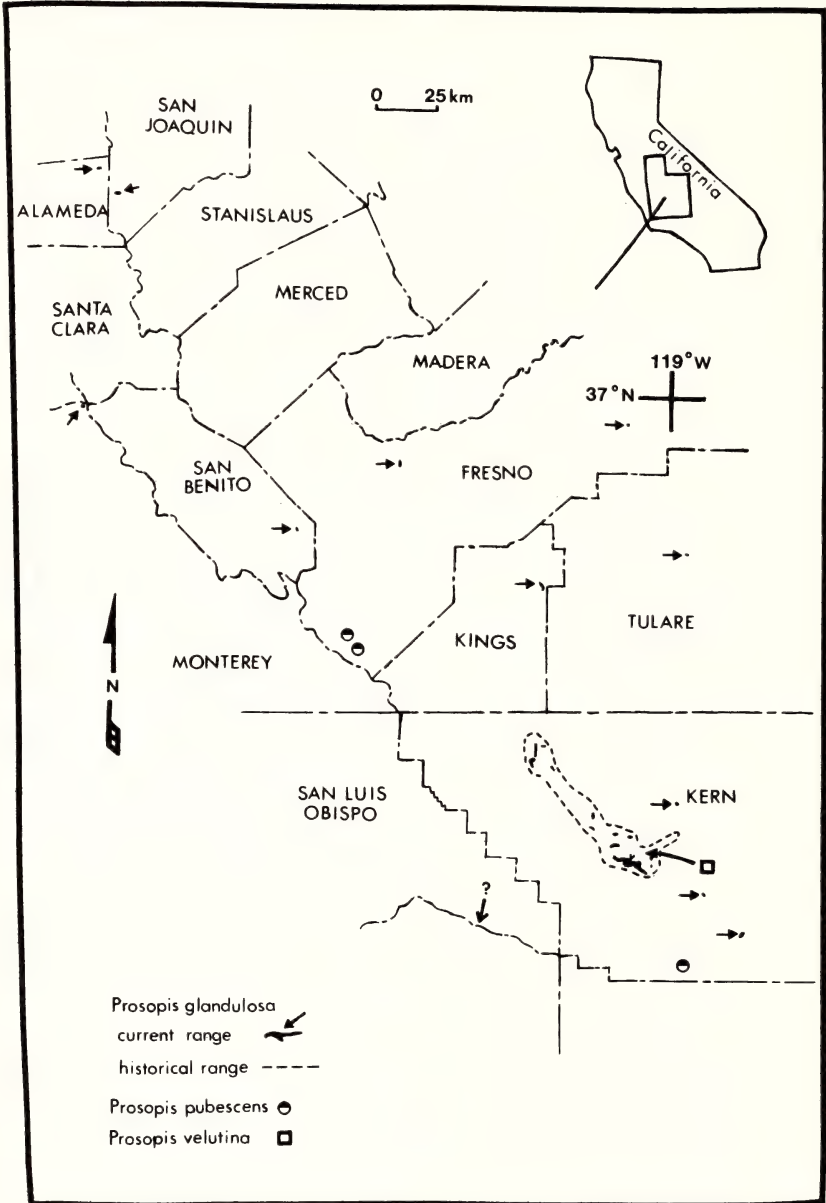


FIG. 1. Distribution of various species of *Prosopis* in the San Joaquin Valley, California. → = isolated populations, usually of less than 10 trees. ? = unvouchered occurrence in the vicinity of the Cuyama River, San Luis Obispo Co.

of the Ton Tache [south of present-day Alpaugh], and through them with the great northern lake [Tulare Lake]. The surrounding country is sterile and unproductive when not an absolute swamp . . . nothing can be conceived more inappropriate than its name, for no place can be imagined more forlorn or desolate in appearance". Traveling north by way of the east side of Goose Lake Slough, Derby continued his appraisal of the region, noting that it was of "precisely the same character throughout—barren, decomposed soil with no trace of vegetation but a few straggling *Artemesias* [presumably *Allenrolfea* or *Atriplex*], except on the margins of the creeks". Given Derby's attention to details of the flora in areas such as the Tule River and Poso Creek, it seems curious that he would fail to note the presence of a plant as conspicuous as mesquite, now one of the largest and relatively common elements of the flora in this area (Fig. 2).

The account of W. H. Brewer (Farquhar 1966) concerning the area of Corral Hollow (San Joaquin and Alameda cos.) is fairly detailed, noting the species and relative abundance of trees in an area where they are often scarce. Again there is no mention of mesquite or even anything that might resemble it.

War Department surveys in the 1850's (Williamson 1853) for a railroad route through the Central Valley and their botanical collections also failed to document or note the presence of mesquite, as did the botanical portion of the California Geological Survey of the area (Gray 1876). In 1983, I retraced most of the route followed by the railroad survey and noted the occurrence of mesquite in at least two areas. A vegetational survey (Davy 1898) of the "waste lands" (alkali sink areas) southwest of Bakersfield in 1896 failed to note the presence of mesquite. The first published reference confirming the presence of *P. glandulosa* in this area was that of Linton (1908), noting that along Buena Vista Lake "on the north shore for several miles is an alkaline desert with an occasional patch of mesquite and sage."

I examined over 100 photographs taken from the late 1880's to the early 1900's in the hypothesized area of establishment and was unable to identify anything that resembled mesquite, although other native taxa (*Populus*, *Salix*, *Allenrolfea*) were readily observable.

There is a consistent lack of herbarium collections from the proposed areas of origin during the time period of concern. This is a weak argument, as the number and scope of collections from the SJV were limited, and the collectors were often more concerned with annuals and smaller perennials (Eastwood 1893). The earliest known collection is a specimen of *P. glandulosa* from the area of Button-willow, Kern Co., collected in 1914 (CAS #65104).

A paucity of paleobotanical information exists concerning the flora of the valley floor at the time of the presumed invasion and estab-



FIG. 2. *Prosopis*-*Atriplex* association near the former site of Buena Vista Lake and in the approximate vicinity of the route traversed by Derby's party.

lishment of many Mojavean elements. Available information does not indicate that mesquite was present in areas near Buena Vista Lake (Mason 1944). Mesquite did reach the "rim" of the San Joaquin Valley in the Pliocene, however, as indicated by fossil material from the vicinity of Tehachapi, at the current western edge of the Mojave Desert (Axelrod 1950). Analyses of fossil pollen records in Arizona have documented the long-term existence of mesquite (Martin 1963), but I was unable to find any core sample data from the area and time period of concern for this study.

ETHNOBOTANICAL EVIDENCE

The seed pods of *P. glandulosa* are and were used widely as a food source by the aboriginal inhabitants of the southwestern United States and adjacent Mexico, and the fibers were utilized to some extent in basketry. The area around Buena Vista and Tulare lakes was inhabited by various groups of the Valley Floor Yokuts (Latta 1949). Ethnographers, e.g., Alfred Kroeber and Frank Latta, have gained valuable insights into the ecology of California aboriginals, which included their uses of the native flora. Latta's (1949) study of the Yokut culture made no mention of the use of mesquite despite an otherwise extensive compendium of food, fiber, and medicinal plants. Driver (1937) questioned members of Central Valley and

Death Valley tribes about their use of mesquite. Responses from the tribes of Death Valley and adjacent areas indicated extensive use, whereas there were no such indications from Valley Floor peoples. Furthermore, use of mesquite fibers in baskets among tribes of the Mojave Desert was documented but was conspicuously lacking among Valley Floor tribes (Merrill 1923).

ENVIRONMENTAL DISTURBANCE

The areas in which I suspect *P. glandulosa* and *P. pubescens* initially became established have an extensive history of environmental disturbance, both human-induced and otherwise (floods, drought). This situation may have fostered the establishment of mesquite. I suggest that in the interval from 1870–1890 *P. glandulosa* became established in the area between Bakersfield and Buena Vista Lake. The hypothesized mechanism of establishment was ingestion of seed pods by cattle in areas where mesquite occurs naturally followed by transport of those cattle by rail to the SJV, defecation by the cattle, and subsequent germination of the seeds. Benson (1941) implicated this mechanism in the establishment of mesquite in Louisiana and Missouri. I suspect a similar situation led to the establishment of *P. pubescens* in the vicinity of Coalinga in western Fresno Co. Darrell Zwang (pers. comm.), a long-term (70+ yr) resident of the area, noted that cattle transport was nonstop, increasing the probability that this mechanism occurred. The seeds of *P. velutina* are known to remain viable for extended periods of time (44 yr) (Martin 1948), which also increases the probability of establishment. If mesquite was carried as fodder in cattle cars, establishment might be due to incidental release into the habitat.

The establishment of mesquite in these and similar sites was probably facilitated by at least two types of environmental disturbances. Many areas in which *Prosopis* occurs are situated in flood plains or washes that are periodically inundated or have high water tables. Prior to the construction of Isabella Dam in 1952, much of the Buena Vista Lake area was unsuitable for continuous agricultural use due to recurrent flooding. In certain areas of the southwest, similar situations have fostered the establishment of extensive mesquite-dominated communities (Minckley and Clark 1984).

Heavy grazing has been shown to facilitate the establishment and spread of mesquite (Glendening 1952, Martin 1975). The number of cattle in Kern Co. increased over 500% between 1870–1880, and an additional 350% from 1880–1890. By the 1890's, approximately 16% of all the cattle in California were being grazed in Kern Co. (Burcham 1957). Further spread of *Prosopis* may have been facilitated by the ingestion of seed pods from maturing trees and movement of cattle to other areas. Populations in Alameda and Fresno

cos. may have become established as the result of deliberate plantings.

ECOLOGICAL CONSIDERATIONS

The ecology of the two species of *Prosopis* lends support to this hypothesis of establishment. *Prosopis glandulosa* and *P. pubescens* are known to invade disturbed areas, particularly in association with drought and overgrazing (Caraher 1970, Herbel et al. 1972, Cable 1973). The physiognomy of an area such as the Santa Rita Experimental Range in Arizona (Martin 1973) can change to such an extent in as little as 50 yr that to those unfamiliar with the original appearance of the site, mesquite might appear to be a "normal" dominant. Historical (Hastings and Turner 1965) and recent (Minckley and Clark 1984) evidence of this type has been noted in the appearance of mesquite-dominated floodplains in Arizona.

I have observed extensive, apparently suitable habitat for mesquite in the SJV, and, thus, it is curious that I have found neither species more widespread. For example, several large canyons with similar relief and soil conditions occur to the north and south of the Fresno Co. populations of *P. pubescens*, but the species is not known from any of these.

Prosopis glandulosa formerly covered an estimated 25–35 km² in the Old River area of Kern Co. (Bill Asserson, pers. comm.), where it coexisted with a mixture of *Allenrolfea occidentalis*, *Suaeda moquinii*, *Atriplex polycarpa*, and *A. lentiformis*. Estimates by Werschull et al. (1983) indicate that the *Prosopis*–*Atriplex* association covered over 57,000 ha at its peak. Based upon my research, I estimate that at most, only 20,000–25,000 ha in the SJV supported mesquite in any association, and of this only 8000–12,000 ha supported high-density stands. Given the extensive areas that have seemingly suitable soil and climatic characteristics and the invasive abilities of this group, I estimate that the potential range for *Prosopis* spp. in the SJV and vicinity was or is greater than 75,000 ha. I suggest that this area has not been occupied due to insufficient time for the species to spread since their advent in the late 1800's. Additionally, massive habitat alteration and concurrent destruction of many populations by humans has slowed the spread.

CURRENT STATUS

The status of mesquite populations in the SJV is of concern to conservationists who consider the *Prosopis*–*Atriplex* association to be a threatened plant community (Jack Zaninovich, pers. comm.). Construction of the Central Valley Water Project and the California Aqueduct resulted in the conversion of a considerable percentage of the remaining wildlands of the Central Valley to agricultural use.

Mesquite-dominated communities were estimated to cover approximately 20,000 ha in Kern Co. in 1963 (CDFG 1965), but patterns of land use over the next 20 yr were projected to reduce this cover to zero. Major reductions in the habitats supporting mesquite did take place over this time interval: approximately 2000 ha remained in Kern Co. in 1979 (Bill Asserson, pers. comm.), and 6500 ha remained in the Tulare basin as a whole (Werschkull et al. 1983). I estimate that as of summer 1986 about 5000 ha of habitat supporting *P. glandulosa* remained in the SJV. Of this, only 15–20% supports vigorous populations. Lowering of water tables in many areas may result in the decline of this species.

I estimate the amount of habitat supporting *P. pubescens* to be less than 1000 ha (primarily in Warthan Canyon), and the number of trees probably does not exceed a few hundred. The status of the populations in Los Gatos Canyon and San Emigdio Canyon is unknown. *Prosopis velutina* probably is represented by only a few trees in the vicinity of Bakersfield (Hilu et al. 1982).

Populations of *Prosopis* are commonly sympatric with other genera of native plants, including *Atriplex*, *Allenrolfea*, *Cephalanthus*, *Salix*, and *Suaeda*. Destruction of mesquite populations will necessarily entail the alteration of a large percentage of the remaining areas of native vegetation in the southern (San Joaquin) valley. For example, the largest remaining population of *P. glandulosa* occurs along the lower Kern River southwest of Bakersfield. Approximately 1100 ha of this area is being developed as a ground-water recharge facility for the City of Bakersfield. This action will eliminate most of the native habitat containing mesquite (Stetson Engineers 1983).

CONCLUSIONS

Historical, ethnobotanical, and ecological evidence indicate that one or both species of mesquite may have naturalized recently (<120 yr) in the SJV. This is equivocal, however, as “. . . I have never seen, and never shall see, that the cessation of the evidence of existence is necessarily evidence of the cessation of existence” (de Morgan 1906). The question of status might be resolved through paleobotanical evidence or core sampling that documents the presence of the species well prior to the hypothesized period of establishment (1870–1890). Mesquite, however, may deposit several growth rings per year (Tom Griggs, pers. comm.), which may frustrate efforts to date individuals.

Monitoring of mesquite populations in the southern SJV is of primary importance. Valuable scientific opportunities will be lost with their further decline or elimination. If the species are indeed native, the chance will be lost to study their associations with floral elements that do not occur elsewhere. If my recent-invasive hy-

pothesis is correct, the destruction of mesquite-dominated communities represents the loss of an unusual opportunity to better understand the nature of historical habitat disturbance and invasive plant ecology.

ACKNOWLEDGMENTS

Inquiries concerning specimens of *Prosopis* were conducted at the following herbaria—Bakersfield Junior College, California Department of Food and Agriculture, California State College—Bakersfield, Merced Junior College, CAS, CSLA, CSPU, DS, FSC, LA, OBI, POM, RSA, SJSU, UC, and UCSB. I thank Daniel Axelrod, Jim Bartel (USFWS), Annetta Carter, Elizabeth Coley, W. J. Ferlatte, Wayne Ferren, Marc Hayes, James Jackson, Robert Jaeger, William Reese, Barry Tanowitz, and an anonymous reviewer for editorial comments. I also thank Bill Asserson (CDFG), Lyman Benson, Ben Chichester, Tom Griggs, Khirdir Hilu, Howard Latimer, Maynard Moe, John Stebbins, Jack Zaninovich, Darrell Zwang, and the curators of the herbaria noted. This paper is dedicated to the memory of Lt. John Reed (CDFG) who gave his life in the protection of California's natural resources.

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ANNOUNCEMENT

1987 AWARDS PRESENTED BY ASPT

The George R. Cooley Award for 1987 was presented to Robert Wyatt of the University of Georgia, Athens, for his paper co-authored with Ireneusz J. Odrzykoski and Ann Stoneburner entitled "Allopolyploidy in bryophytes: recurring origins of *Plagiomnium medium*." The award is given annually by the American Society of Plant Taxonomists for the outstanding contributed paper in plant systematics presented at the annual meeting.

The fourth Asa Gray Award was presented to Reed C. Rollins of Harvard University, Cambridge, Massachusetts. The Asa Gray Award is given by the American Society of Plant Taxonomists to honor an individual "for outstanding accomplishments pertinent to the goals of the Society." The award has been presented to Rogers McVaugh at the 1984 meeting, Arthur Cronquist at the 1985 meeting, and Lincoln Constance at the 1986 meeting.

SOME NEW AND RECONSIDERED CALIFORNIA *DUDLEYA* (CRASSULACEAE)

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ABSTRACT

Three new taxa of *Dudleya* from California are described: *Dudleya cymosa* subsp. *agourensis*, *D. cymosa* subsp. *crebrifolia*, and *D. abramsii* subsp. *affinis*. Three new combinations of *Dudleya* also are proposed from California: *D. cymosa* subsp. *pumila*, *D. cymosa* subsp. *paniculata*, and *D. abramsii* subsp. *calicola*. *Dudleya gigantea* is reduced to a synonym of *D. cymosa* subsp. *cymosa* and *D. minor* is reduced to a synonym of *D. lanceolata*. A neotype is designated for *Echeveria cymosa* Lem. (= *D. cymosa* subsp. *cymosa*).

Recent collections made during a study of the *Dudleya cymosa*–*abramsii* complex revealed some undescribed taxa and a need to re-evaluate others. *Dudleya* species often exhibit considerable phenotypic plasticity resulting from the variability of climatic conditions, soil, and exposure that often alters, sometimes quite dramatically, the appearance of the same plant from year to year. Although morphological measurements taken from the field are important to accurately identify many plants, field measurements from succulent plants like *Dudleya* often have proven to be unreliable. Therefore, the interpretation of each taxon discussed here will rely heavily on data obtained from cultivated plants in an effort to reduce variability in certain morphological characters (e.g., leaf size and shape, floral stem length, inflorescence shape, pedicel length, etc.) that are used in determining taxa. This approach makes it possible to evaluate under a uniform and stable environment those characters that apparently are controlled genetically.

MATERIALS AND METHODS

In collecting live material for study, five plants were selected by tossing a 10 cm hoop within an area greater than 9 m² where there were many flowering plants of *Dudleya*. The first five plants selected were measured in the field and then collected for cultivation studies.

Herbarium and living specimens were examined. Most of the floral measurements were obtained from wild or cultivated living material. Because of the tendency for certain flower parts, in particular the staminal filaments, of *Dudleya* to continue to grow even after the

flower appears to be fully mature, all measurements were taken two days following anther dehiscence.

Cultivated plants were grown at Hawthorne, California (33°55'N, 118°22'W), in a structure constructed with a clear fiberglass roof and 30% shade cloth for the sides. An artificial soil was used that consisted of two parts fine redwood shavings, two parts coarse Canadian peat moss, two parts diatomaceous earth, one part sand, and one part fine perlite. One kg of milorganite was incorporated for each m³ of medium. The medium was then moistened and aged for a minimum of one month.

Flower buds used for cytological observations were collected from cultivated plants between 0930 and 1000 hr and fixed in a modified Carnoy solution (Uhl and Moran 1953), which consisted of chloroform, EtOH, and glacial acetic acid (3:2:1, v/v/v). Counts were made from a minimum of five buds.

TAXONOMIC TREATMENT

- DUDLEYA CYMOSA (Lemaire) Britton & Rose subsp. CYMOSA—*Echeveria cymosa* Lemaire, *Revue Hortic.* 7:439. 1858.—*Cotyledon cymosa* Baker in Saunders, *Refug. Bot.* 1:pl. 69. 1869.—*Dudleya cymosa* Britton & Rose, *Bull. N.Y. Bot. Gard* 3:21. 1903.—*Cotyledon laxa* var. *cymosa* Jepson, *Man. Fl. Pl. Calif.* 453. 1925.—*Echeveria laxa* var. *cymosa* Jepson, *Fl. Calif.* 2:114. 1936.—Neotype: Plate in Saunders, *Refug. Bot.*, pl. 69. 1869.
- Dudleya gigantea* Rose in Britton & Rose, *op. cit.* p. 23.—*Cotyledon gigantea* Fedde, *Bot. Jahresber. Just.* 31:826. 1904.—*Echeveria amadorana* Berger in Engler & Prantl, *Nat. Pflanzen fam.*, ed. 2, 18a:479. 1930 (based on *Dudleya gigantea* Rose).—TYPE: USA, CA, Amador Co., New York Falls, ca. 1500 ft (460 m), 15 Jun 1896, *G. Hansen* 2012 (Holotype: US! (US 338497), photo LA!; isotype: CAS!, NY!).
- Echeveria lanceolata* var. *incerta* Jepson, *Fl. Calif.*, p. 115. 1936.—TYPE: USA, CA, Calaveras Co., Calaveritas Creek, near Kentucky House, ca. 900 ft (275 m), 27 May 1923, *W. L. Jepson* 9919 (Holotype: JEPS!, photo LA!).

Caudex short, usually less than 5 cm long, 1–3.5 cm diam., unbranched or few branched. Basal rosettes 6–20(–25) cm diam., consisting of 6–25 oblanceolate to rarely spatulate leaves, acute, acuminate or, infrequently, cuspidate, 2–17 cm long, 1.5–6 cm wide, and 1–5 mm diam. Floral stem 0.5–4.5 dm tall, 2–8 mm diam., with 7–20(–30) horizontal to ascending ovate to triangular-lanceolate leaves, acute to acuminate, the lowermost 0.5–3(–10) cm long and 5–15 mm wide. Inflorescence obpyramidal, infrequently paniculate or simple, commonly with 2–4 branches that rebranch 0–3 times; cincinnus circinate when young, ascending in age, 1–5(–15) cm long

and (1-)2-10(-20) flowers; pedicels erect, the lowermost 5-15 mm long, 0.5-2 mm diam. Calyx 3-7 mm long, 2.5-6 mm wide, rounded to truncate below; lobes triangular to triangular-ovate, acute to \pm acuminate, 1.5-5 mm long, 1.5-4 mm wide. Corolla ovoid in bud, cylindrical in anthesis, often with the petal apices spreading from 45°-90°; petals yellow, orange, or red, occasionally glaucous along the midrib, elliptic to narrowly lanceolate, acute, 7-15 mm long, 2-4 mm wide, connate 1-2.5 mm; filaments 4-8.5 mm long, adnate for 1-3.5 mm, the epipetalous mostly 0.5 mm shorter and adnate, mostly 0.5-0.7 mm higher than the antesealous; anthers yellow, 1-2 mm long. Gynoecium 4-10 mm long, erect when young, slightly spreading in age, ovaries 3-8 mm long, styles 1-2 mm long. Nectaries reniform, 1-2 mm wide. Chromosome number: $n = 17$. Flowering April to July.

Distribution. USA, California: Coast Ranges from Humboldt Co. to Santa Clara Co.; Sierra Nevada. Elev. 100-2700 m.

Based on the original description, the type locality is probably in California ("... corolles jaune-pâle. Californie? Très distincte!"—Lemaire 1858). According to Moran (1951), no authentic specimen is available; however, he noted that Lemaire's plant came from the horticulturist Louis de Smet of Ledeburg, Belgium, in or before 1858, and the plant illustrated by Baker in *Saunders Refugio Botanicum* came from a horticulturist in nearby Ghent in 1855 and probably was of the same introduction. Because the plate compares well with the original description and clearly illustrates most of the plants presently referred to *Dudleya cymosa*, this plate serves as the neotype until an authentic type specimen is found.

Based on its greater average size when compared with *D. cymosa* subsp. *cymosa*, Moran (1951, 1957) recognized *Dudleya gigantea* as a subspecies of *Dudleya cymosa*. Moran (1951) noted, however, that there was a dwarf specimen on the type sheet. He also mentioned that subsp. *cymosa* occurs at nearby localities, with no evident natural barriers. As a result of additional collections and the data from cultivation, the size difference between *D. gigantea* and *D. cymosa* is not apparent and, thus, there is not enough evidence to warrant maintaining *D. gigantea* as a distinct taxonomic entity.

Moran (1951, 1960) reduced *Echeveria lanceolata* var. *incerta* to a synonym of *Dudleya cymosa* subsp. *gigantea*. Variety *incerta* also does not appear to be different from *D. cymosa* subsp. *cymosa*.

Dudleya cymosa* subsp. *pumila (Rose) K. Nakai, comb. nov.—*Dudleya pumila* Rose, Bull. N.Y. Bot. Gard. 3:14. 1903.—*Cotyledon pumila* Fedde, Bot. Jahresber. Just. 31:826. 1904.—*Echeveria parva* Berger in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 18a: 477. 1930 (based on *Dudleya pumila* Rose).—TYPE: USA, CA,

San Bernardino Co., San Bernardino Mtns., between Green Valley and Deep Creek, 7000 ft (2120 m), 19 Jul 1899, *H. M. Hall* 1350 (Holotype: US!, photo DS!, LA!; isotype: UC!).

Distribution. USA, California: South Coast Ranges from Monterey Co. south to the San Gabriel and San Bernardino mtns. Elev. 100–1800 m from Santa Barbara Co. north, 600–2600 m from Ventura Co. south.

Rose (1903) based *D. minor* on two collections [*Rose* 421 (ex *Hasse*) (NY, US), 1893 *McClatchie* (NY, UC)]; both were collected from San Gabriel Canyon. Moran (1957) reduced *D. minor* to a subspecies of *D. cymosa*. Munz (1959, 1974) lists *D. cymosa* subsp. *minor* from the Santa Lucia Range in Monterey Co. south into the Transverse Range of southern California.

I was unable to find any dudleya resembling the many herbarium specimens labeled *D. minor* or *D. cymosa* subsp. *minor* (Rose) Moran at the type locality. Although the original description suggests a relationship with *D. cymosa* based on leaf shape, pedicel length, and petal shape, I have determined that the holotype of *D. minor* resembles plants intermediate between *D. cymosa* and *D. lanceolata* (Nutt.) Britt. & Rose.

In southern California, *D. cymosa* is usually a small plant, mostly 5–8 cm in diameter. In the central portion of the Transverse Ranges, the rosette leaves are mostly oblanceolate to spatulate. The floral stem is usually less than 15 cm tall, the inflorescence is rather compact with 4–8 flowers per cincinnus. The lowermost pedicels are often at least as long as the length of the corolla. *Dudleya cymosa* is a diploid ($n = 17$; Uhl and Moran 1953).

Dudleya lanceolata is often larger, 8–12 cm in diameter. The rosette leaves are typically oblong to lanceolate or infrequently elliptic to ovate. The floral stem is usually greater than 15 cm tall, the inflorescence is often lax with 6–15 flowers per cincinnus. The lowermost pedicels may be as long as the corolla, but usually they are much shorter. *Dudleya lanceolata* is a tetraploid ($n = 34$; Uhl and Moran 1953).

The shape of the basal rosette leaves and the length of the pedicels of the holotype of *D. minor* suggest a relationship with *D. cymosa*, whereas the length of the floral stem, the more lax inflorescence, and the greater number of flowers per cincinnus is similar to *D. lanceolata*. Indeed, most of the dudleyas observed from elevation 500–1000 m were clearly *D. lanceolata*; however, a few individuals resemble *D. cymosa* morphologically even though cytologically they were tetraploids.

For comparison of *Dudleya minor* with *D. cymosa* and *D. lanceolata*, dudleyas were collected along California State Highway 39, which travels through San Gabriel Canyon, at elevational increments

of 100 m from 500–1700 m. Morphological measurements were made in the field. The plants were then cultivated and the same measurements were repeated the following year and chromosome counts were made. The measurements were translated into numerical values or scores so that the sum of the total characters from each population may be compared (Table 1, Fig. 1). Voucher specimens were deposited at LA.

Figure 1 shows there is a distinct break in morphological measurements between 1200–1500 m. Wild plants from 500–1200 m had an average score of 11.5, whereas those from 1500–1700 m had an average of 18.7. Cultivated plants displayed a similar break, although less than that found in wild plants (13.3 vs. 19.0). The chromosome number also correlated with elevation. Tetraploid plants occurred below 1200 m and diploid plants occurred above 1500 m. Based on morphology and chromosome number, *D. lanceolata* apparently occurs from 500–1200 m and *D. cymosa* is found above 1500 m in San Gabriel Canyon.

Although the type specimen of *D. minor* may resemble *D. cymosa*, it was collected below 1200 m. Thus, on the basis of morphological and cytological data obtained from both wild and cultivated plants I consider *D. minor* to be conspecific with *D. lanceolata*. Because the type specimen of *D. pumila* Rose represents most of the *D. cymosa* in southern California, I propose the combination *D. cymosa* subsp. *pumila* to replace *D. cymosa* subsp. *minor*.

- Dudleya cymosa** subsp. **paniculata** (Jeps.) K. Nakai, comb. nov.—*Cotyledon caespitosa* var. *paniculata* Jeps., Fl. W. Mid. Calif. 267. 1901.—*Dudleya paniculata* Britt. & Rose, Bull. N.Y. Bot. Gard. 3:27. 1903.—*Cotyledon paniculata* Fedde, Bot. Jahresber. Gard. 31:826. 1904 (non *C. paniculata* Thunberg.).—*Echeveria jepsonii* Nelson & Macbride, Bot. Gaz. (Crawfordsville) 56:477. 1913 (based on *Cotyledon caespitosa* var. *paniculata* Jeps.).—*Cotyledon laxa* var. *paniculata* Jeps., Man. Fl. Pl. Calif. 543. 1925.—*Echeveria laxa* var. *paniculata* Jeps. Fl. Calif. 2:114. 1936.—TYPE: USA, CA, Alameda Co., Morrison Canyon, 20 Jun 1897, W. L. Jepson 13419 (Holotype: JEPS!, photo LA!).
- Dudleya humilis* Rose, Bull. N.Y. Bot. Gard. 3:27. 1903.—*Cotyledon humilis* Fedde, Bot. Jahresber. Just. 31:826. 1904 (non *C. humilis* Marloth. 1915).—*Echeveria diaboli* Berger in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 18a:480. 1930 (based on *Dudleya humilis* Rose.).—TYPE: USA, CA, Contra Costa Co., summit of Mt. Diablo, 2 Jun 1903, Alice Eastwood s.n. (Rose 620) (Holotype: US!, photo LA!; isotype: NY!).

Distribution. Inner South Coast Range from Contra Costa Co. south to western Fresno and northeastern Monterey cos.

Moran (1951, 1960) considered *Cotyledon caespitosa* var. *paniculata* a synonym of *Dudleya cymosa* subsp. *setchellii* (Jeps.) Moran. He noted, however, that they might be separated on the basis of the rosette leaf shape. Based on studying 34 herbarium specimens and 100 live plants from 20 populations of subsp. *paniculata* and 13 herbarium specimens and 20 live plants from four populations of subsp. *setchellii*, I found that subsp. *paniculata* differs from subsp. *setchellii* by having oblong to oblanceolate basal rosette leaves compared with oblong-triangular leaves, an inflorescence of 2–3 branches that rebranch one or twice rather than 2–3 mostly simple branches, and pedicels 6–12 mm long versus 4–7 mm long. Subspecies *setchellii* is restricted to the serpentine rock outcrops within the Santa Clara Valley, whereas subsp. *paniculata* occurs within the Inner South Coast Range on various rock substrates.

Dudleya humilis Rose is reduced to a synonym of *D. cymosa* subsp. *paniculata*. A similar form [K. Nakai 816 (LA)] was collected near the summit of Mt. Hamilton, which is south of Mt. Diablo, the type locality of *D. humilis*. *Dudleya humilis* appears to be an edaphic dwarf of subsp. *paniculata* because cultivated plants I have grown from each location did not appear different from cultivated plants of subsp. *paniculata*.

***Dudleya cymosa* subsp. *agourensis* K. Nakai, subsp. nov.**

A subspecies typica caulis ramosus, rosulae foliis 6–10, glaucis, ellipticis vel oblongis differt. Figs. 2a,b, 5.

Plants simple or with six or more cespitosely branched rosettes 5–10 cm diam., with 6–10 elliptic to oblong glaucous leaves. Basal rosette leaves 3–10 cm long, 1–1.5 cm wide, acute to acuminate; cauline leaves lanceolate, glaucous, 1–2.5 cm long, 7–10 mm wide, acute to acuminate. Floral stem erect, 10–20 cm tall, glaucous, often tinged with red; inflorescence of 2–3 simple to bifurcate branches; cincinnus ascending, 1–3 cm long with 3–8 flowers; lowermost pedicels 6–12 mm long. Petals bright yellow, occasionally glaucous along the midrib, petal apex spreading 45–90°. Chromosome number: $n = 17$. Flowering May to June.

TYPE: USA, CA, Los Angeles Co., Santa Monica Mtns., ca. 0.5 km s. of the junction of Agoura and Cornell roads on Cornell Road, 34°08¼'N, 118°45½'W, on nw.-facing volcanic rock road embankment, locally abundant, 275 m. Associated with *Malosma laurina*, *Haplopappus linearis*, *Dichelostemma pulchella*, *Delphinium parryi*, *Calochortus venustus*. 27 May 1980, K. Nakai 606 (Holotype: CAS; isotype: LA, SD).

PARATYPES: Los Angeles Co., w. of Calabasas Moran 3472 (UC); Agoura, along Cornell Road, Nakai 436 (LA); n.-facing volcanic

TABLE 1. MORPHOLOGICAL MEASUREMENTS, DESCRIPTIONS, CHROMOSOME NUMBERS, AND SCORE OF *Dudleya cymosa* AND *D. lanceolata* COLLECTED ALONG CALIFORNIA STATE HIGHWAY 39 IN SAN GABRIEL CANYON AT 100 m INTERVALS. W = measurements and descriptions from wild plants; C = measurements and descriptions from cultivated plants; s.d. = standard deviation; score is the sum of all morphological measurements and descriptions when converted into a numerical value. The vegetative measurements and descriptions with their corresponding scores are as follows: 1) Maximum basal rosette diameter (cm): 1-5 = 3, 6-10 = 2, 10-15 = 1. 2) The average shape of the basal rosette leaves: lanceolate to oblong = 1, elliptic to ovate = 2, oblanceolate to spatulate = 3. 3) The average length of the basal rosette leaves (in cm): 1-5 = 3, 5-10 = 2, 10-15 = 1. 4) The average floral stem length (in cm): 1-10 = 3, 10-20 = 2, 20-30 = 1. 5) The shape of the inflorescence: lax or open = 1, compact = 2. 6) The average number of flowers per cincinnus: 3-7 = 3, 7-11 = 2, 11-15 = 1. 7) The average length of the pedicel (in mm): 5-7 = 1, 7-9 = 2, 9-12 = 3.

[illegible]

TABLE 1. CONTINUED.

Elevation (m)	Rosette dia- meter (cm)		Rosette leaf shape	Rosette leaf length (cm)		Floral stem length (cm)		Inflorescence	Number of flowers per cincinnus		Lowermost pedicel length (mm)		Chro- mo- some num- ber (n)	Score	
	\bar{x}	s.d.		\bar{x}	s.d.	\bar{x}	s.d.		\bar{x}	s.d.	\bar{x}	s.d.			
1000 none found															
1100															
W	12.0	2.5	oblong to oblanceolate	10.3	2.0	19.3	6.2	lax		13.5	5.3	6.0	0.0	11	
C	6.0	0.5	oblong to	3.5	0.7	11.0	3.1	lax		8.0	2.5	6.0	0.0	34	12
1200															
W	13.0	3.6	ovate to lanceolate	11.5	3.8	13.4	2.5	lax		11.0	4.2	8.5	1.0	12	
C	10.0	1.1	oblanceolate	7.5	0.5	11.0	3.1	lax to compact		9.3	2.1	10.0	1.0	34	14
1300 none found															
1400 none found															
1500															
W	6.5	1.5	rhombic- oblanceolate to spatulate	4.3	0.8	6.5	1.0	compact		6.0	2.0	10.0	0.5	18	
C	5.5	1.5	spatulate to rhombic	4.0	0.8	4.0	0.8	compact		5.0	2.0	11.0	1.0	17	20
1600															
W	6.0	0.8	spatulate	5.3	0.5	7.0	1.7	compact		5.5	3.0	9.5	1.5	18	
C	6.0	0.8	spatulate	5.5	0.4	3.5	0.7	compact		6.0	1.0	10.0	1.0	17	18
1700															
W	4.5	0.9	spatulate	3.0	0.6	4.5	0.9	compact		6.0	2.5	11.0	1.0	20	
C	4.5	0.9	spatulate	3.0	0.6	3.0	0.3	compact		4.0	1.0	9.0	1.0	17	19

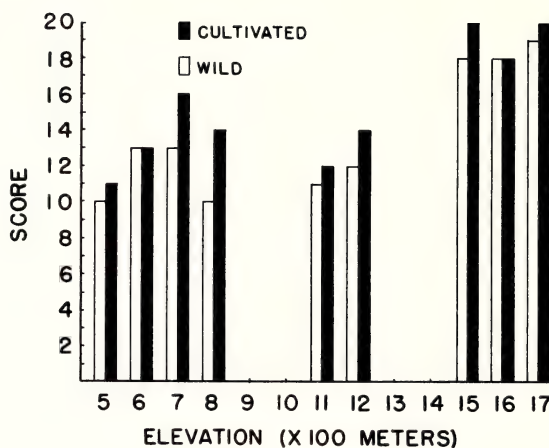


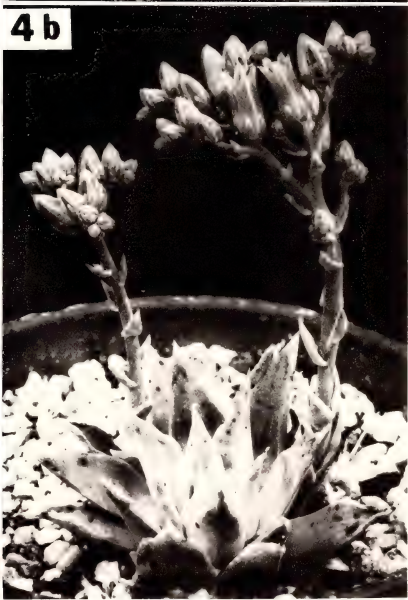
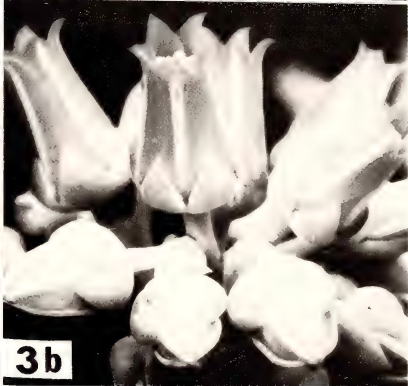
FIG. 1. Bar graph illustrating index score vs. elevation derived from Table 1 for *Dudleya cymosa* and *D. lanceolata* as collected from along California State Highway 39. □ = wild plants; ■ = cultivated plants.

slopes of Ladyface Mountain, 400 m, *Nakai 1119* (CAS, LA); rocks on the e. side of State Hwy. 23 near the jct. of Portrero Road and Hwy. 23, 365 m, *Nakai 512* (LA). Ventura Co., n.-facing volcanic rock along Hwy. 23 e. of Lake Eleanor, 300 m, *Nakai 607* (CAS, LA).

Distribution. North slope of the western portions of the Santa Monica Mtns.

Dudleya cymosa subsp. *agourensis* differs from subsp. *cymosa* by having rosettes consisting of 6–10 elliptic to oblong leaves rather than 10–25 leaves that are oblanceolate to spatulate. Uhl and Moran (1953) placed a population of subsp. *agourensis* (Moran 3472) with *D. cymosa* subsp. *ovatifolia* (Britt.) Moran. Nakai (1983) considered this population a distinct race of subsp. *ovatifolia*. Subspecies *ovatifolia* also occurs in the Santa Monica Mountains and, like subsp. *agourensis*, it possesses yellow petals and rosettes of 6–10 leaves. Subspecies *ovatifolia*, however, differs from subsp. *agourensis* by its unbranched caudex, ovate to elliptic basal rosette leaves, green with

→
FIGS. 2–4. Photographs of new taxa in *Dudleya*. 2. *Dudleya cymosa* subsp. *agourensis* K. Nakai. a. Isotype plant (0.4×). b. Inflorescence in detail (1.25×). 3. *Dudleya cymosa* subsp. *crebrifolia* Nakai & Verity. a. Holotype plant (0.2×). b. Inflorescence in detail (2×). 4. *Dudleya abramsii* subsp. *affinis* K. Nakai. a. Inflorescence in detail (1.25×). b. Isotype plant (0.5×).



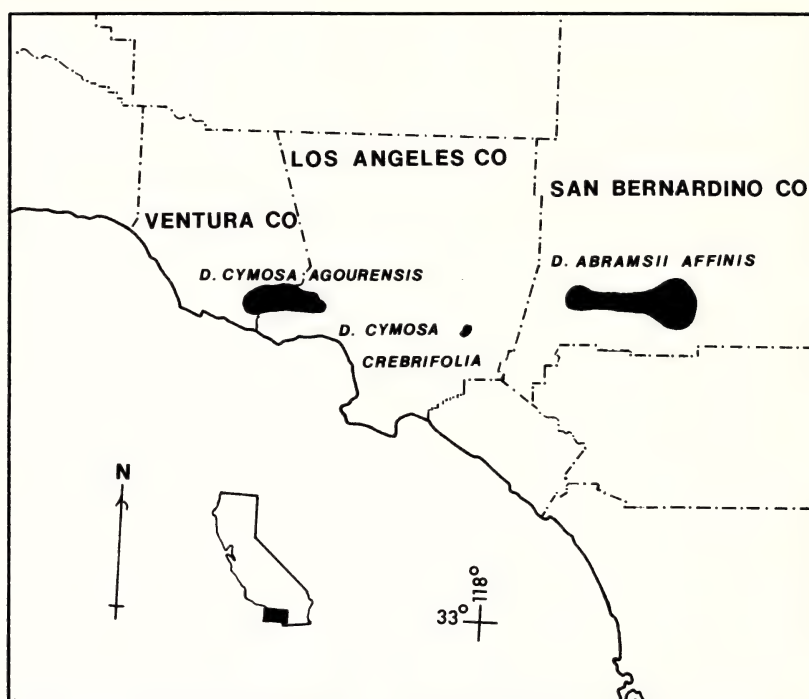


FIG. 5. Geographic distribution of *Dudleya cymosa* subsp. *agourensis*, *D. cymosa* subsp. *crebrifolia*, and *D. abramsii* subsp. *affinis*.

a maroon suffusion on the underside, slightly longer pedicels, and petal apices spreading 90° or more. Subspecies *ovatifolia* is found on the southern slopes of the Santa Monica Mountains on shaded sedimentary rock slopes. In contrast, subsp. *agourensis* is found on the northern slopes of the range on drier, exposed west- to northwest-facing rock outcrops.

Dudleya verityi K. Nakai, also found in the Santa Monica Mountains, has flowers similar to subsp. *agourensis*. This species differs from subsp. *agourensis* by its paler flowers, several to many dichotomously branched stems that may elongate to more than 10 cm long rather than the one or infrequently several cespitosely branched stems that are mostly less than 5 cm long.

***Dudleya cymosa* subsp. *crebrifolia* Nakai & Verity, subsp. nov.**

A subspecies typica caulis simplex, foliis caulis floriferi multibus et crebribus et tardiflorentem differt. Figs. 3a,b, 5.

Caudex 1–2 cm diam. with simple to rarely few branched basal rosettes, 5–12 cm diam., with 6–15 spreading to ascending leaves.

Basal rosettes leaves mostly elliptic to spatulate, acute to acuminate, 4–10(–15) cm long, 2–5 cm wide near the middle, olive-green, rarely glaucous, slightly maroon on the undersurface. Floral stem 10–30(–n50) cm tall, yellowish-green, with 20–50 close-set, horizontal, alternate to subopposite leaves. Inflorescence obpyramidal, with 2–4 branches that branch 1–2 times; cincinnus 2–10 cm long, with 2–15 flowers, pedicels 3–8 mm long. Petals mustard yellow, midribs glaucous, elliptic, acute, 9–10 mm long, 3–3.5 mm wide at the middle, connate 1–1.5 mm, apices spreading to 45°. Chromosome number: $n = 17$. Flowering late June to July (August).

TYPE: USA, CA, Los Angeles Co., San Gabriel Mtns., Fish Canyon, 34°11'N, 117°55½'W, ca. 1.5 km nw. from the mouth of the canyon on n.-facing granitic slopes, common, 400 m. Associated with: *Alnus rhombifolia*, *Umbellularia californica*, *Toxicodendron diversilobum*, *Dudleya lanceolata*, and *D. densiflora*. 25 Jun 1981, K. Nakai 775 (Holotype: CAS; isotype: LA, MO, RSA, SD, US).

PARATYPES: Los Angeles Co., Fish Canyon, *Davidson 3578* (US), *Hood 43-77k* (LA), *Nakai 361* (CAS, LA), *776* (CAS, LA).

Distribution. San Gabriel Mtns., Fish Canyon, 0.5–4 km from the mouth of canyon.

Subspecies *crebrifolia* is distinguished by its mostly solitary basal rosette with mostly elliptic to spatulate leaves, the large number of cauline leaves that are often crowded, and a later flowering period. At the higher elevations (2000 m or more), subsp. *crebrifolia* may still be in flower as late as late July, but when cultivated, it flowers from April to early June. In a letter at US to J. N. Rose (25 Jun 1923), A. Davidson suggested that this plant may be new and noted that one plant had 13 floral stems and the basal rosette leaves were 6 inches (15 cm) long. Subspecies *crebrifolia* is known only in Fish Canyon on vertical granite slopes on both walls of the canyon in partly shaded areas.

Subspecies *crebrifolia* apparently is related most closely to *D. cymosa* subsp. *pumila* and is well within the range of subsp. *pumila*. Although its basal rosettes are often larger than those of subsp. *pumila* from the San Gabriel Mountains, the size is within the overall limit of subsp. *pumila* when plants from the entire geographic range of the latter are compared. Subspecies *crebrifolia* differs from subsp. *pumila* by its elliptic leaves, longer floral stem with 2–3 times the number of cauline leaves that are often crowded together, and a flowering period that is usually 4–6 weeks later. Subspecies *crebrifolia* occurs from 350–600 m, whereas subsp. *pumila*, in the San Gabriel Mountains, occurs below 750 m only in the northern portion of the range [Elizabeth Lake Cyn., elev. 675 m, *Nakai 1015* (LA); elev. 610 m, *Nakai 1016* (LA)].

In Fish Canyon, *D. lanceolata* is common and occasionally grows sympatrically with subsp. *crebrifolia*. *Dudleya lanceolata* is similar

to subsp. *crebrifolia* in basal rosette size, length of the floral stem, and petal color. Infrequently, the number of cauline leaves in *D. lanceolata* is similar to those of subsp. *crebrifolia*. *Dudleya lanceolata* differs from subsp. *crebrifolia* in its lanceolate, often glaucous, leaves, a more lax inflorescence, and an earlier flowering period. *Dudleya lanceolata* is tetraploid ($n = 34$), whereas subsp. *crebrifolia* is a diploid.

DUDLEYA ABRAMSII Rose subsp. **ABRAMSII**—*Dudleya abramsii* Rose in Britton & Rose, Bull. N.Y. Bot. Gard. 3:14. 1903.—*Cotyledon abramsii* Fedde, Bot. Jahresber. Just. 31:826. 1904.—*Echeveria abramsii* Berger in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 18a:477. 1930.—TYPE: USA, CA, San Diego Co., wet crevices of rocks west of Jacumba, 1 Jun 1903, *Leroy Abrams 3707* (Holotype: US!, photo LA!; isotype: DS!, GH!, NY!, POM!, UC!, US!).

Caudex diameter 1–3 cm thick, mostly less than 5 cm long, unbranched or 5–20(–75) cespitose branches. Basal rosette 2–8(–15) cm diam. consisting of 8–25 erect or ascending oblong-lanceolate, acute to acuminate, glaucous leaves, apiculate, 1–10 cm long, 3–15 mm wide, 1–4 mm diam., plane or concave ventrally, rounded dorsally, the base 5–15 mm wide. Floral stem 2–25 cm tall, 1–5 mm diam. Cauline leaves 3–20, ascending, triangular-lanceolate, acute, the lowermost 0.5–3 cm long, 2–11 mm wide. Inflorescence of 2–3 simple to once or twice bifurcate ascending branches or obpyramidal. Cincinnus 3–15 cm long, with 2–10(–20) flowers. Pedicels erect, 0.5–5(–11) mm long. Calyx 3–5 mm wide, 3–6 mm high, subtruncate to tapered below, the segments triangular-ovate to lanceolate, acute, 2–5 mm long, 1.5–3 mm wide. Petals pale yellow, often with red vertical lines particularly along the midrib, elliptic to narrow lanceolate, acute, occasionally erose, erect with petal apices often spreading to 90°, 8–13 mm long, 2–3 mm wide, connate 1–4.5 mm. Epipetalous filaments 2.5–6 mm long, adnate 1–3 mm; antesepalous filaments 4.5–8 mm long, adnate 2–4 mm; anthers yellow, 1–1.5 mm long. Gynoecium erect, slender, attenuate, 4–7 mm high, ovary 3–5.5 mm long, styles 0.5–2 mm long. Nectaries reniform, pale yellow, 0.5–1 mm long. Chromosome number: $n = 17$. Flowering April to June.

Distribution. USA, CA, Riverside Co., San Jacinto Mtns., San Diego Co., Laguna Mtns.; MEXICO, Baja California Norte, Sierra Juarez and Sierra San Perdo Martir. Elev. 750–1750 m.

The label data from the type specimens varies, and thus, the exact type locality is uncertain. The holotype and an isotype specimen at NY, both of which are a plant cultivated by Rose, are labeled “five miles [6.7 km] west of Jacumba”. The specimen at POM, however,

is labeled "Walker's Ranch, near Jacumba". Others, including an isotype at US, are labeled "two miles [2.7 km] west of Jacumba". Because Abrams spent most of his academic career at Stanford University, one would suspect that the specimen at DS would have an accurate label. I was able to collect *D. abramsii* 2 mi west of Jacumba, but I was unable to find it 5 mi west of Jacumba.

Moran (1951) listed two populations of *D. abramsii* from the San Jacinto Mountains, one from near Kenworthy [Munz 5788 (POM)] and the other from Tahquitz (sic) Ridge, 9000 ft (2770 m) [Jaeger in 1921 (POM)]. The population near Kenworthy is *D. abramsii*, but differs from typical *D. abramsii* by lacking the characteristic red striations along the petal midrib. The specimen from Tahquitz Ridge differs considerably from the Kenworthy population in its comparatively broad, oblong to ovate leaves and short floral stem. It resembles no specimens of *D. abramsii* that I have studied. The "Tahquitz" specimen, however, does resemble plants of *D. cymosa* subsp. *pumila*. A recent collection made near Tahquitz Ridge by J. Catlin [Lily Rock, near Idlywild, 2300 m, Nakai 984 (CAS, LA)] has reddish flowers and is similar to the "Tahquitz" specimen. Catlin (pers. comm.) reports similar plants on Suicide Rock, across Strawberry Valley from Lily Rock, and along Snow Creek on the north slope of San Jacinto Peak. The status of these populations is uncertain until more material can be studied, but it appears they are not *D. abramsii*.

Dudleya abramsii subsp. **calcicola** (Bartel & Shevock) K. Nakai, comb. nov. — *Dudleya calcicola* Bartel & Shevock, Madroño 30: 210. 1983. — TYPE: USA, CA, Tulare Co., Kern River at Roads End, T23S R32E S13, Sequoia National Forest, 1200 m, 11 Jul 1981, Shevock 8802 (Holotype: CAS!, photo LA!; isotype: FSC, NY!, RSA!, SBBG, SD!, UC).

Distribution. USA, CA, southern Sierra Nevada from the Rincon area south of Durrwood Creek in Tulare Co. to the southern Piute Mtns. in Kern Co. Elev. 500–1550 m.

Collections I have made from the Piute Mountains, the vicinity of Lake Isabella, and along the Kern River suggest that *D. calcicola* is closer to *D. abramsii* than previously believed. Bartel and Shevock (1983) suggested that *D. calcicola* was intermediate between *D. abramsii* and *D. cymosa*, but closer to *D. abramsii*. They noted that *D. calcicola* was distinct from *D. abramsii* in its 1) heavier foliar bloom, 2) obpyramidal inflorescence with a thicker floral stem and spreading cincinni versus a comparatively simple inflorescence and ascending cincinni, 3) slightly longer pedicel, 4) pale yellow petals unmarked with red, and 5) occurrence predominately on limestone.

The type locality of *D. calcicola* is the limestone outcrops above

Roads End along the Kern River in Tulare Co., but I have observed plants resembling *D. calcicola* at a number of localities along the Kern River on substrates other than limestone. For example, one population was found less than 0.5 km north of the type locality on metamorphic rock. Pedicel length from cultivated plants from 12 populations of *D. abramsii* and 13 populations of *D. calcicola* exhibited no differences. They measured 3–7 mm (\bar{X} = 5 mm) for *D. abramsii* and 3–8 mm, (\bar{X} = 5 mm), for *D. calcicola*. Measurements made from herbarium specimens, however, ranged from 2–10 mm (\bar{X} = 5 mm), for *D. abramsii* and from 2–12 mm (\bar{X} = 6 mm) for *D. calcicola*. Although several populations of *D. calcicola* do have flowers with plain, pale yellow petals, others have the characteristic *D. abramsii* red striations along the petal midrib. Cultivated plants I collected from the type locality and observed for five flowering seasons had flowers with petals conspicuously marked with red. In at least three populations of *D. abramsii* [MEXICO, Baja California Norte, Cerra Blanco, *Moran 17608* (SD); 2 km w. of Rancho Santa Cruz, Sierra San Pedro Martir, *Moran 23461* (SD), *Nakai and Prigge 1136* (CAS, LA); USA, CA, Riverside Co., Kenworthy, *Munz 5788* (POM, SD), *Nakai 1007* (CAS, LA)] the petals lack red pigment. The density of the foliar bloom does not appear to differ between the two taxa.

Typical *D. calcicola* is a densely-packed plant with up to 50 rosettes. Bartel and Shevock (1983), however, cite populations (e.g., Long Canyon) that have plants with one to a few rosettes. In the Laguna Mountains of San Diego Co., the higher elevation populations of *D. abramsii* also have plants with 50 or more rosettes, and a population of a *D. abramsii* subsp. *affinis* K. Nakai in Cushenbury Canyon has densely-packed plants with up to 50 rosettes. Thus, the number of rosettes per plant may not differ between the taxa.

An important character in which *D. calcicola* is similar to *D. abramsii* is the relative lengths of the antesealous and epipetalous stamens. In *D. cymosa*, the difference in staminal length is often small (<0.5 mm). In both *D. abramsii* and *D. calcicola*, the difference is usually 1–1.5 mm. This strongly supports a close relationship between *D. calcicola* and *D. abramsii*.

Another character that distinguishes *D. calcicola* from *D. abramsii* is the inflorescence. Although the inflorescence of *D. calcicola* found in the wild may be similar to *D. abramsii*, cultivated plants consistently have an obpyramidal inflorescence consisting of 2–4 branches that bifurcate once or twice. Cultivated plants of *D. abramsii* have a simpler inflorescence of 2–3 mostly simple branches. Cultivated *D. calcicola* tends to have more cauline leaves (8–15) in comparison to *D. abramsii* (2–8).

Although there are enough differences to warrant taxonomic recognition, the two taxa have considerable overlap in most of the key

characters. Of additional interest are two collections from the geographic range of *D. calcicola* that were identified by authorities as *D. abramsii*: one from the Tehachapi Mtns. [May 1925, Davidson 3599 (US)], annotated by Rose; another collected by J. Zavinowich from Jawbone Canyon on the east slope of the Piute Mtns. [Moran 24196 (SD)], determined by Moran. These two authorities on *Dudleya* apparently also recognized the resemblance of this material to *D. abramsii*. Thus, I proposed the combination *D. abramsii* subsp. *calcicola*.

***Dudleya abramsii* subsp. *affinis* K. Nakai, subsp. nov.**

A subspecies typica caudice simplicis, foliis rosulae oblanceolatis vel ellipticis differt. Figs. 4a,b, 5.

Plants simple, rarely cespitosely branched. Basal rosette 3–6 cm diam., of 10–25 oblanceolate to elliptic, glaucous leaves, 2–4 cm long, 7–15 mm wide; apices acute to acuminate. Cauline leaves lanceolate, glaucous, 5–6 mm long, 2–3 mm wide, acute. Floral stem erect, 5–11 cm long, pale yellow to glaucous. Inflorescence of 2–3 mostly simple branches, cincinnus ascending, 2–8 cm long, with 3–8 flowers, lowermost pedicels 2.5–8 mm long. Petals pale yellow with red striations along the midribs, connate 1.5–2.5 mm, apices spreading to 90°. Epipetalous filaments 2.5–4 mm long, antesealous filaments 3.5–6 mm long. Chromosome number: $n = 17$. Flowering May to July.

TYPE: USA, CA, San Bernardino Co., San Bernardino Mtns., Green Canyon, ca. 0.5 km sw. of National Forest Road 2N93 on trail to Sugarloaf Mountain where the trail crosses the creek, 34°13'N, 116°48'W, on e. side of creek on granite; common; 2600 m; with *Juniperus*, *Pinus*, *Cercocarpus*, *Echinocerus*. 28 Jun 1984, K. Nakai 1146 (Holotype: CAS; isotype: LA, NY).

PARATYPES: USA, CA, San Bernardino Co., confluence of Deep and Hook creeks, Nakai 1110 (CAS, LA), 1114 (CAS, LA, RSA); Holcomb Creek, 8 km sw. of Big Pine Flat, Nakai 1153 (LA); nw. slope of Gold Mountain, 3.2 km w. of Big Bear refuse dump, Nakai 1151 (CAS, LA); n. shore of Lake Baldwin, D. B. Stark 4992 (RSA), Nakai 702 (CAS, LA); Johnson Grade, Peirson 8972 (POM, UC), Peirce s.n. (POM), Moran 2193 (UC), Nakai 1145 (CAS, LA); ridge e. of Lake Baldwin, Munz 10494 (POM); plateau s. of Lake Baldwin, Peirson s.n. (RSA); Cushenbury Canyon, Deburg 2608 (RSA), Nakai 1147 (CAS, LA); Cushenbury Spring, Parish 1629 (POM); Green Canyon, Clausen & Trapido 4770 (CU, NY, US, WTU), Nakai 1113 (CAS, LA).

Distribution. North slopes of the San Bernardino Mtns. from 1800–2600 m on granite, quartzite, or, rarely, limestone.

Dudleya abramsii subsp. *affinis* differs from subsp. *abramsii* by

its mostly unbranched caudex and basal rosette leaves that are oblanceolate to elliptic rather than oblong-lanceolate. Some plants of subsp. *affinis* resemble *D. cymosa* subsp. *pumila*, particularly in rosette size, leaf shape, and, in more robust plants, the inflorescence. The most consistent differences are a shorter pedicel length, pale yellow petals with red striations, and the difference in length between the antesealous and epipetalous stamens.

Plants from Cushenbury Canyon grow on limestone and differ from typical plants of subsp. *affinis* by their several to many branched caudex and smaller rosettes, 1.5–3 cm in diameter. This population seems similar to subsp. *calcicola* and subsp. *abramsii*. It differs from subsp. *calcicola* by its more simple inflorescence and from subsp. *abramsii* by its rosette leaf shape. Although this population is intermediate between these three subspecies of *D. abramsii*, I presently consider this population an aberrant form of subsp. *affinis*.

KEY TO SPECIES AND SUBSPECIES

- A. Pedicels 5–20 mm long; petals connate 1–2.5 mm; the difference between epipetalous and antesealous staminal length is usually <0.5 mm.
 - B. Basal rosette leaves evergreen, 2–17 cm long, 0.5–6 cm wide; caudex more than 1 cm diam.
 - C. Floral stem mostly 1.5–4.5 dm tall.
 - D. Floral stem with 20–50 close-set leaves; basal rosette leaves elliptic to spatulate. San Gabriel Mtns., s. California *D. cymosa* subsp. *crebrifolia*
 - D. Floral stem usually with <20 leaves; basal rosette leaves oblong-oblanceolate to oblong-triangular, rarely spatulate. Central and n. California.
 - E. Petals bright yellow to red; rosette leaves oblong-oblanceolate, rarely spatulate, 1–6 cm wide. Coast Range from the Salinas River, Santa Clara Co., n. to Humboldt Co.; Sierra Nevada
..... *D. cymosa* subsp. *cymosa*
 - E. Petals pale yellow.
 - F. Basal rosette leaves oblong to oblanceolate; inflorescence of 2–3 bifurcate branches; pedicels 6–12 mm long. Inner South Coast Range from Contra Costa Co., to w. Fresno and ne. Monterey cos., on various rock substrates
..... *D. cymosa* subsp. *paniculata*
 - F. Basal rosette leaves oblong-triangular; inflorescence of 2–3 simple branches; pedicels 4–7 mm long. Santa Clara Valley on serpentine ...
..... *D. cymosa* subsp. *setchellii*

- C. Floral stem mostly < 1.5 dm tall. Outer South Coast Range from the Salinas River s. to s. California.
 - G. Basal rosette leaves oblanceolate to spatulate, usually 10–25, mostly short acuminate to cuspidate. Outer South Coast Range to San Gabriel and San Bernardino mtns. *D. cymosa* subsp. *pumila*
 - G. Basal rosette leaves oblong to elliptic or ovate, usually 6–10, acute to acuminate.
 - H. Basal rosette leaves ovate, green, often with a maroon suffusion on the underside; caudex unbranched. Santa Monica and Santa Ana mtns. *D. cymosa* subsp. *ovatifolia*
 - H. Basal rosette leaves oblong to elliptic, glaucous; caudex simple or few to, rarely, several branches. Santa Monica Mtns. *D. cymosa* subsp. *agourensis*
- B. Basal rosette leaves withering in summer, 1.5–4 cm long, 5–12 mm wide; caudex < 1 cm diam. *D. cymosa* subsp. *marcescens*
- A. Pedicels 0.5–7 mm long; petals connate 1.5–4.5 mm; the difference between the epipetalous and antesepalous staminal length is usually 1–1.5 mm.
 - I. Basal rosette leaves oblong to oblong-lanceolate; plants with few to many branches.
 - J. Inflorescence of 2–3 mostly simple branches; pedicels mostly < 5 mm long; petals usually with red striations along the midribs.
 - K. Lower cauline leaves usually < 15 mm long; floral stem 2–15 cm tall; petals connate 2–4.5 mm. San Jacinto Mtns., Riverside Co., and Laguna Mtns., San Diego Co.; Sierra Juarez and Sierra San Pedro Martir, Baja California Norte *D. abramsii* subsp. *abramsii*
 - K. Lower cauline leaves 10–30 mm long; floral stem 5–25 cm tall; petals connate 1.5–3 mm. San Luis Obispo Co. *D. abramsii* subsp. *murina*
 - J. Inflorescence of 2–3 simple to usually bifurcate branches; pedicels 3–8 mm long; petals with or without red striations along the midribs. Southern Sierra Nevada *D. abramsii* subsp. *calcicola*
 - I. Basal rosette leaves elliptic to oblanceolate; plants usually unbranched. San Bernardino Mtns., San Bernardino Co. *D. abramsii* subsp. *affinis*

Additional specimens of *Dudleya* that were cultivated and examined but not cited in the text. Collection numbers, unless otherwise noted, are the author's.

DUDLEYA ABRAMSII: subsp. ABRAMSII—USA, CA, Riverside Co.; San Jacinto Mtns.,

near Kenworthy, 1059. San Diego Co.: Mt. Laguna, 454; Laguna Mtns., Kwaaymit Pt., 1180; Descanso Junction, 845; Kitchen Creek, 844; Corte Madera Lake, *Van Der Werff s.n.*; Campo 840; Jacumba, 841; Dubber Spur, 842. MEX, Baja Calif. Norte: Sierra Juarez, near Laguna Hansen, *Prigge 5098*; n. of Valle Trinidad, *Verity s.n.*; Sierra San Pedro Martir, between Mike Sky Ranch and El Burro, *Verity s.n.*; s. of Rancho Santa Cruz, *Nakai and Prigge 1136*. Subsp. *CALCICOLA*—USA, CA, Tulare Co.: ½ km n. of Road's End, 1080; Road's End, 825; Hospital Flat Campground, ca. 9.5 km n. of Kernville, 1078. Kern Co.: 2.0 km s. of Kernville, 1077; 8 km s. of Kernville, 827; Long Canyon, 828; near Mountain Mesa, 829; Bodfish Cyn., 830; s. of Bodfish, 831; near Twin Oaks, 678; near Loraine, 679, 680; Caliente, 832; Cottonwood Creek, near Kelso Valley, 676, 677.

DUDLEYA CYMOSA: subsp. *CYMOSA*—USA, CA, Mendocino Co.: Hopland, *McCabe 356*. Sonoma Co.: near Mt. St. Helena, *Almeda s.n.*; Cazadero, 973. Marin Co.: Bolinas Bay, 975; Stinson Beach 398; s. of Stinson Beach, 398; Mt. Talmapais, 399. Solano Co.: s. of American Cyn. Rd., 821; Mix Cyn., Vaca Mtns., 531. Santa Cruz Co.: Eagle Rock, *McCabe 369*. Santa Clara Co.: Lexington Reservoir, 814; New Almaden, 814; Loma Prieta, 813; Stevens Creek, 1088. Tehama Co.: near Paynes Creek, 961. Sierra Co.: w. of Downieville, *McCabe 507*. Nevada Co.: near Nevada City, 951. Placer Co.: Applegate, 950. Amador Co.: near Ione, 532; w. of Volcano, 394; Volcano, 534; near Mokelumne River, 535. Calaveras Co.: near San Andreas, 536; near Kentucky House, 393, 537. Tuolumne Co.: Table Mtn., 1087; near Coulterville, 538. Mariposa Co.: near Yosemite Valley, 1084, 1085; near Bear Valley, 539, 822. Inyo Co.: Sawmill Creek, 1081. Tulare Co.: near Springville, 392; w. of Pierpoint, 823. Kern Co.: Bear Hollow Creek, 1075; Shirley Creek, 1076. Subsp. *PANICULATA*—Contra Costa Co.: n. slope of Mt. Diablo, 949; Mt. Diablo, 396; s. slope Mt. Diablo, 948. Alameda Co.: Palomare Rd., 820; Welch Creek, 819. Santa Clara Co.: Coyote Reservoir, 818; Alum Rock, 817; Mt. Hamilton, 816; Anderson Reservoir, 977; Coyote Lake, 978. Stanislaus Co.: Arroyo del Puerto, 946, 947. Merced Co.: Pacheco Pass, 945. San Benito Co.: Pinnacles, 809; near Panoche Pass, 944; Clear Creek, 942. Monterey Co.: Lewis Creek, 808; Lorenzo Creek, 628; Bull Cyn., 1092. Fresno Co.: Coalinga Hot Spr., *McCabe 501*. Subsp. *PUMILA*—Monterey Co.: Pine Valley, 526; n. of Castro Cyn., 631; s. of Castro Cyn., 632; n. of Mission San Antonio, 523, 524; Nacimiento-Fergusson Rd., 100 m, 410; Nacimiento-Fergusson Rd., 700 m, 409, 633. Santa Barbara Co.: Santa Barbara Cyn., 788; Rattlesnake Cyn., 1100. Ventura Co.: confluence of Potrero John and Sespe creeks, 544; Sespe Gorge, 545, 789. Los Angeles Co.: Elizabeth Lake Cyn., 825 m, 1013; 790 m, 1014; 670 m, 1015; 610 m, 1016; Arroyo Seco, 915 m, 430; 850 m, 553; 1070 m, 555; Hidden Springs, 383, 427; San Gabriel Cyn., 1500 m, 1125; 1600 m, 1126; 1700 m, 1021. San Bernardino Co.: San Antonio Falls, 1900 m, 689; Waterman Cyn., 386, 1183; s. of Crestline 1184; Miller Cyn., 1185; Little Mill Creek, 700; Keller Mtn., 702, 1143; Skinner Creek, 1148.

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ANNOUNCEMENT

BOTANICAL COLLECTIONS IN MICROFICHE FORM AT UCSB

The UCSB Library and the UCSB Herbarium are pleased to announce the purchase of type and special botanical collections, in microfiche form, from Meckler Publishing. Three collections were acquired through the UC Shared Acquisition Program, which is a University-wide library effort designed to facilitate sharing of unique or expensive materials among the nine UC campuses and Stanford University. The collections include: 1) *New York Botanical Garden Vascular Plant Type Collections*; 2) *Vascular Plant Types and Early Authentic Specimens of the Academy of Natural Sciences of Philadelphia*; and 3) *United States National Herbarium Smithsonian Institution Vascular Plant Types*. Printed indices have been purchased for each campus to help users locate individual specimens. The microfiche are housed in a separate viewing room in the UCSB Library and can be borrowed through interlibrary loan agreements. In addition to those collections purchased through Shared Acquisitions, the UCSB Library has purchased the *California Academy of Sciences Plant Type Collection* in microfiche form. We encourage all interested parties to make use of these important and accessible resources.

ANNOUNCEMENT

NEW PUBLICATION

Jepson Globe: A Newsletter from the Friends of the Jepson Herbarium, vol. 1, no. 1, pp. 1–4, 1987, no ISSN, subscription with contribution of \$15.00 or higher (from Friends of the Jepson Herbarium, Dept. Botany, Univ. of California, Berkeley, CA 94720). [With message by G. L. Stebbins and 2 articles: J. H. Thomas on history of herbaria, pt. 1; J. C. Hickman on status of Jepson Manual Project (text and illus. 15% complete, some 150 collaborators, 3 paid staff, and many volunteers, notably Emily Reid, scientific illustrator).]

CYMOPHORA (ASTERACEAE: HELIANTHEAE)
RETURNED TO *TRIDAX*

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ABSTRACT

Cytological and morphological evidence supports the merger of *Cymophora* B. L. Robinson with *Tridax* L. (Asteraceae: Heliantheae). Chromosome counts of $n = 9$ are reported for *Tridax accedens* Blake and the closely related *T. dubia* Rose. ***Tridax hintonii*** (Turner & Powell) Keil, Luckow & Pinkava, comb. nov., is proposed, based on *Cymophora hintonii* Turner & Powell.

Our chromosome count of $n = 9$ for *Tridax accedens* Blake (Asteraceae: Heliantheae), the first report for this species, provides key information in an ongoing taxonomic controversy. During the past 20 years several researchers have discussed the status of *Cymophora* and its relationship to *Tridax* (Anderson and Beaman 1968, Turner et al. 1973, Turner and Powell 1977, Canne 1977, 1978, 1983, Robinson et al. 1981, McVaugh 1984). Anderson and Beaman noted numerous morphological similarities between *C. pringlei* B. L. Robins. (at the time the only species of *Cymophora*) and two species of *Tridax* (*T. accedens* and *T. dubia*) and concluded that *Cymophora* could not be maintained separate from *Tridax*. They noted that *C. pringlei* differs mainly from the two *Tridax* species in having smaller, fewer-flowered heads and epappose achenes. It is particularly similar to *T. accedens*. They transferred *C. pringlei* into *Tridax* as *T. oligantha* Anderson & Beaman.

Turner et al. (1973) published a chromosome number of $2n = 16$ (counted by Robert Irving) for *T. oligantha* and questioned the relationship of this species to *Tridax* ($x = 9, 10$). They suggested instead a relationship of *Cymophora* to *Galinsoga* ($x = 8$) and *Sabazia* ($x = 4$). They further suggested that a chromosome count for *T. accedens* would be helpful in evaluating the relationship of *T. oligantha*.

Turner and Powell (1977) reinstated *Cymophora* (as a genus distinct from *Tridax*), transferred *T. accedens* to it and described a third species, *C. hintonii* Turner & Powell. They discounted the purported relationship of *T. accedens* to *T. dubia* (Blake 1943, Powell 1965, Anderson and Beaman 1968), but provided neither a key nor discussed the morphological differences between the two genera.

Canne (1977) noted that *Tridax venezuelensis* Arist. & Cuatr., which bears features of both *Galinsoga* and *Tridax*, is morphologically most similar to species placed by Turner and Powell into *Cymophora*, and transferred this species into *Cymophora*. She further noted that the four species of *Cymophora* fall into two well-defined morphological species groups characterized by differences in leaf shape, petiole length and the number of veins in the phyllaries and pales. *Cymophora hintonii* and *C. venezuelensis* form one group, and *C. accedens* and *C. pringlei* the other. Robinson et al. (1981) again noted the similarity of *T. dubia* to *Cymophora*, but questioned the transfer of *T. venezuelensis* into *Cymophora*, suggesting that it represented a different phyletic line than the remainder of *Cymophora*. They reported an approximate count of $2n = \text{ca. } 18$ for *T. venezuelensis*. Robinson (1981) listed *Cymophora* distinct from *Tridax*, but did not discuss its relationships or composition. Canne (1983) reported $n = 9$ for *C. hintonii* which further weakened the chromosomal basis for distinguishing *Cymophora* from *Tridax*.

Two types of evidence have been used to date in studies of the two genera: morphology and chromosome numbers. Anderson and Beaman (1968) and McVaugh (1984) used morphological evidence to support union of *Cymophora* with *Tridax*. Turner and Powell (1977) and Canne (1977, 1978) used a combination of morphological and cytological data to support their separation of the genera. A review of the conflicting sources of evidence is presented below.

MORPHOLOGICAL EVIDENCE

Habit and vegetative morphology cannot be used to separate the two genera. Both genera are composed of opposite leaved herbs. All of the species that have been assigned to *Cymophora* are taprooted annuals. Eleven of the 25 species of *Tridax* (s. str.) are annuals, including *T. dubia*, a species considered to be a link between *Tridax* and *Cymophora* by Anderson and Beaman (1968). Turner and Powell (1977) considered *T. dubia* to be "a true *Tridax*". Canne (1978) listed the following features as distinctive of *Cymophora*: paniculate-cymose capitulescence, zygomorphic outer disc corollas and white corollas. In a tabular comparison of several genera of the Galinsoginae she described the capitulescences of *Tridax* as "heads solitary or in few-headed subcymes" and those of *Cymophora* as "heads in several- to many-headed cymose panicles". Although some *Tridax*

species have solitary heads, *T. dubia* and several other species (e.g., *T. platyphylla*) have many-headed cymose panicles. The capitulescences of *T. dubia* and *Cymophora accedens* are similar in appearance and in number and distribution of heads and were used as evidence of the relationship of these taxa and *C. pringlei* by Anderson and Beaman (1968).

The heads and the included bracts and florets of *Cymophora* species are smaller than those of most *Tridax*. However, *T. dubia* has flowers and bracts similar in size to those of *Cymophora* species. The involuclral bracts of *Tridax* are 2–5 seriate and those of *Cymophora* are 1–3 seriate. The species of *Tridax* most similar to *Cymophora* have involuclral bracts of similar number and form (Anderson and Beaman 1968). The outer florets of both *Cymophora* and *Tridax* heads tend to be zygomorphic. In most *Tridax* species, these flowers are pistillate and have an evident ligule (anterior lip) and are considered to be rays even though a small posterior lip is present. Rays are absent in several species of *Tridax* and in *T. bilabiata* the disc florets are bilabiate. In three *Cymophora* species, the outer florets are perfect and bilabiate with a short anterior lip and are considered to be bilabiate disc florets (Anderson and Beaman 1968, Turner and Powell 1977, Canne 1978). The fourth species, *C. venezuelensis*, has pistillate, bilabiate outer florets that are treated as rays (Canne, 1977). The remaining disc florets are mostly actinomorphic or nearly so in both genera. Disc corollas in *Tridax* species vary from creamy yellow to bright yellow or yellow-green. Those of *Cymophora* are creamy white.

In *Cymophora*, the achenes may bear short fimbriate or plumose scales or may be epappose. The pappus of most *Tridax* species consists of slender plumose or fimbriate scales or bristles. The pappus of *T. dubia*, however, is similar to that of *Cymophora*, which consists of short, fimbriate-margined scales.

CYTOLOGICAL EVIDENCE

Our count of $n = 9$ for *C. accedens* indicates that two (and possibly three) of the *Cymophora* species share a base of $x = 9$. Both morphological groups recognized by Canne contain species with this base number, as does *Tridax* (including *T. dubia*). In addition, it is possible that the single reported count of $2n = 16$ may be inaccurate. Irving, as listed by Turner et al. (1973), reported a chromosome count of $2n = 16$ from mitotic material. Turner (pers. comm.) notes that a crude penciled camera lucida drawing attached to the voucher specimen (seeds of which served as the source material) does suggest a number of $2n = 16$, but some of the chromosomes may be unresolved and, thus, a count of $2n = 18$ might still hold.

Tridax is dibasic with $x = 9$ and 10. The species of *Tridax* most similar to *Cymophora* have $n = 9$.



FIGS. 1, 2. Camera lucida drawings of chromosomes at diakinesis. 1. *Tridax accedens*. 2. *Tridax dubia*.

CONCLUSIONS

We propose here that continued recognition of *Cymophora* as a genus distinct from *Tridax* is not supported by either morphological or cytological evidence. The closest relatives of *Cymophora* appear to be species of *Tridax* and the morphological characters that separate the genera are weak if they exist at all. Of the characters listed by Canne (1978), only the color of the disc corollas seems to stand up to scrutiny. The cymose paniculate capitulescence of *Cymophora* species is fundamentally similar to the capitulescences of several *Tridax* species. Rayless heads with bilabiate outer disc florets occur in *T. bilabiata* and in *Cymophora* species. We agree with those who consider *T. dubia* and *T. accedens* to be closely related, and, therefore, arrive at the same conclusion as Anderson and Beaman (1968). We suggest that all four species of *Cymophora* be returned to *Tridax*.

McVaugh (1984) arrived at a similar conclusion. Noting the lack of morphological differences between *Cymophora* and *Tridax*, he placed *C. accedens* back into *Tridax*. He did not propose, however, a combination in *Tridax* for *C. hintonii*, but merely listed it (as *Cymophora hintonii*) among the species of *Tridax* in Nueva Galicia. We, therefore, propose the following combination:

Tridax hintonii (Turner & Powell) Keil, Luckow & Pinkava, comb. nov.—*Cymophora hintonii* Turner & Powell, Madroño 24:2. 1977.

We report the following chromosome counts and the voucher specimens that document them:

Tridax accedens S. F. Blake. $2n = 9_{II}$ (Fig. 1). MEXICO: Colima: Hwy. 110, 17 mi ne. of jct. with Hwy. 200, Keil and Luckow 15139 (OBI).

Tridax dubia Rose. $2n = 9_{II}$ (Fig. 2). MEXICO: Jalisco: 8 mi n. of El Tuito, Keil and Luckow 15112 (OBI).

ACKNOWLEDGMENTS

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NEW MADROÑO EDITOR

The Executive Council of the California Botanical Society is pleased to announce the appointment of Dr. David J. Keil to the position of Editor of *Madroño*. Dr. Keil, Professor of Botany, is the Director of the Robert F. Hoover Herbarium (OBI). His editorship will commence in January 1988 with volume 35. All new manuscripts submitted to *Madroño* and all returned revisions should be mailed to him at the Biological Sciences Department, California Polytechnic State University, San Luis Obispo, CA 93407. Mr. Wayne R. Ferren, Jr., who has completed his tenure as Editor, will be appointed to the Board of Editors to assist with continuity of journal management.

VASCULAR PLANTS OF EASTERN IMPERIAL COUNTY, CALIFORNIA

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ABSTRACT

An annotated catalogue of the vascular flora was compiled from field collections and herbarium records from the eastern third of Imperial Co., California, including wetland habitats along the lower Colorado River. The study area is located in the Lower Colorado Valley subdivision of the Sonoran Desert, an arid area with little elevational relief. The flora is correspondingly depauperate, with only 278 native species recorded from 2050 km², including 56 species found only in wetland habitats along the lower Colorado River. Ecological and floristic factors that contribute to the low diversity include a relative lack of habitat differentiation among desert species and the lack of a well developed herbaceous perennial flora.

The Lower Colorado Valley subdivision of the Sonoran Desert (Shreve 1951) in eastern Imperial Co., California, is one of the driest parts of the desert region of the southwestern United States and northwestern Mexico. It is perhaps also the most poorly known area botanically in California. The objective of this study was to catalogue the flora of this area, emphasizing the desert habitats and the wetland habitats along the lower Colorado River. This area was selected for study because it is centered within a section of the Sonoran Desert for which no other local floras have been compiled; the data were used in a broader study of the floristics of the southwestern U.S. (McLaughlin 1986).

STUDY AREA

The study area includes most of Imperial Co. east of 115°W longitude (Fig. 1). The Riverside Co. line and the International Boundary form the northern and southern boundaries, respectively; the eastern boundary is the Colorado River. Wetland habitats along both river banks are included in the study area. The western boundary excludes the Algodones Dune field, which has its own distinctive

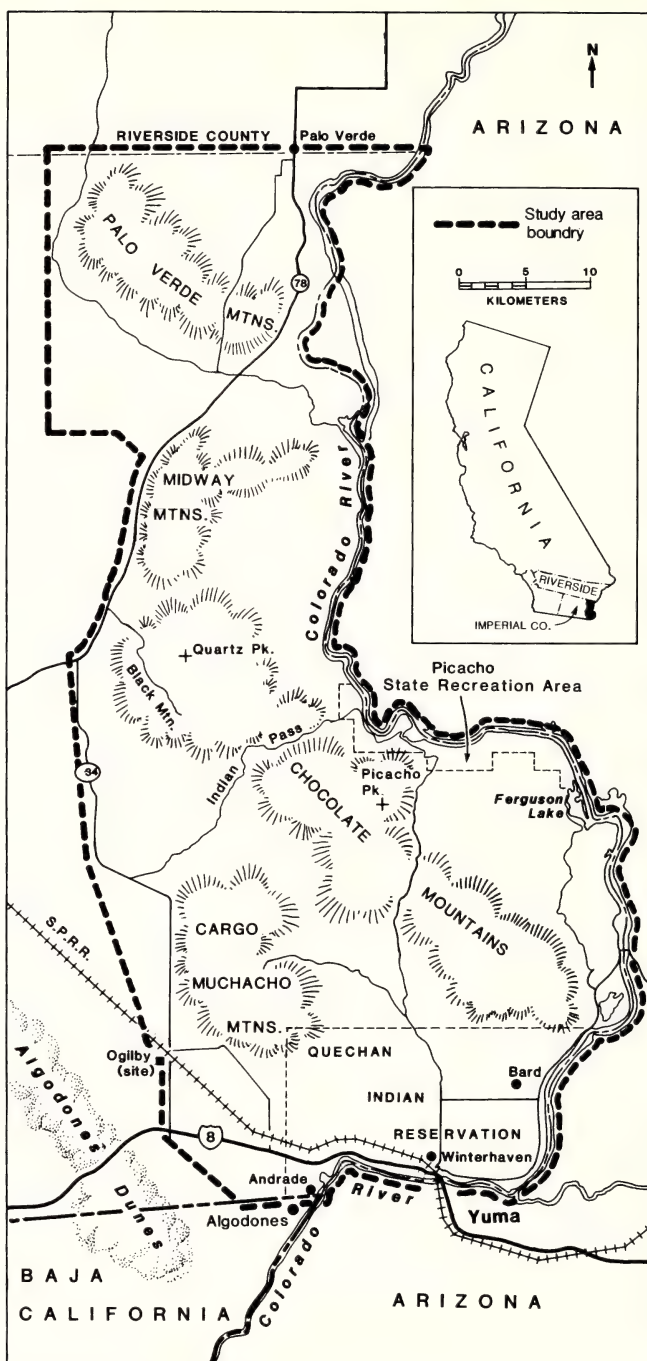


FIG. 1. Map of study area in eastern Imperial Co., extreme southeastern corner of California.

TABLE 1. CLIMATIC DATA FOR STATIONS ADJACENT TO STUDY AREA (WILLMOTT ET AL. 1981).

Station	Lat.	Long.	Elev. (m)	Mean monthly temperature (°C)		Precipitation (mm)	
				Jan	Jul	Winter Oct– Mar	Sum- mer Apr– Sep
Amos, CA	33°6'	115°13'	78	12.4	35.2	40	21
Blythe, CA	33°36'	114°36'	82	10.2	32.6	63	37
Brawley, CA	32°59'	115°32'	–36	11.4	32.3	47	15
Mexicali, B.C.	32°39'	115°39'	4	11.8	33.0	48	23
Quartzsite, AZ	33°40'	114°15'	147	10.1	34.0	77	70
Yuma, AZ	32°44'	114°37'	42	12.4	32.8	53	31

flora (Bowers 1984), and the Chocolate Mountains Naval Gunnery Range, to which access is restricted.

The study area is approximately 2050 km². Elevations range from near sea level to 664 m at Quartz Peak in the Chocolate Mountains. The major mountain ranges in the area include the Palo Verde Mountains in the north, the Cargo Muchacho Mountains in the southwest, and the Chocolate Mountains that form an irregular mass trending northwest to southeast across the center of the area. Picacho Peak, a distinctive landmark 29 km north of Yuma, lies in the Chocolate Mountains.

The climate of the study area is extremely arid (Table 1). Annual rainfall varies from about 60 mm in the southwest corner to about 100 mm in the higher elevations. Most of the rain occurs in the winter; late summer storms in September account for most of the rain that falls from April through October. Mean daily maximum summer temperatures are 38–41°C; winter temperatures seldom drop below freezing.

VEGETATION AND HABITATS

Deserts

The vegetation of the Lower Colorado Valley subdivision of the Sonoran Desert has been described by Shreve (1925, 1951) and Turner and Brown (1982). Because of the extreme aridity of the area, the vegetation is remarkably monotonous. Undisturbed sections of the desert on mountain slopes, bajadas, and sandy flats are all dominated by *Larrea tridentata*–*Ambrosia dumosa* microphyllous desert (Shreve 1951). The low-lying, fine-textured soils of the Colorado River floodplains that are currently under cultivation—the eastern

half of the Quechan (formerly Ft. Yuma) Indian Reservation and the Palo Verde Valley—were probably once extensive *Atriplex* flats (Turner and Brown 1982).

Mountains, slopes, and flats. A group of about a dozen woody and succulent species are dominant on mountain tops, steep, rocky slopes (Fig. 2), gentle slopes (Fig. 3), and sandy and gravelly flats (Fig. 4). These species are: *Larrea tridentata*, *Ambrosia dumosa*, *Encelia farinosa*, *Hilaria rigida*, *Opuntia acanthocarpa*, *O. basilaris*, *O. bigelovii*, *Cercidium floridum*, *Fouquieria splendens*, *Krameria grayi*, *Lycium andersonii*, and *Fagonia laevis*. A few species are confined mostly to broad, sandy washes (Fig. 5): *Justicia californica*, *Bebbia juncea*, *Chilopsis linearis*, *Acacia greggii*, *Olneya tesota*, *Psoralea spinosa*, *Lycium fremontii*, and *L. torreyi*. Fewer species are confined to the relatively mesic, steep, north-facing slopes within the study area: *Pleurocoronis pluriseta*, *Salazaria mexicana*, and *Galium stellatum*. Several are found only in broad, sandy washes and north-facing slopes, suggesting that the two habitats are similar in their moisture availability. Included in this last group are *Ambrosia ilicifolia*, *Trixis californica*, *Hyptis emoryi*, *Condalia globosa*, and *Zizyphus obtusifolia*.

The common annuals also display a low degree of habitat differentiation. Many species occur in washes, on sandy and gravelly flats, on rocky slopes of all aspects, and on mountain tops. Common species include *Oligomeris linifolia*, *Lupinus arizonicus*, *Camissonia brevipes*, *C. refracta*, *Chaenactis carphoclinia*, *Phacelia crenulata*, *Mentzelia involucrata*, *Mohavea confertiflora*, *Cryptantha angustifolia*, *Plantago fastigiata*, and *Eriogonum thomasi*.

Desert pavement and riverine dunes. Two habitats of special interest are desert pavement and riverine dunes. Desert pavement refers to unusually barren flats covered by a closely-packed layer of pebbles, which usually have a well-developed coating of desert varnish (Musick 1975). Pavement soils are typically saline and sodic and have very low infiltration rates. They are consequently the driest habitats in the desert. Shrubs, mostly *Larrea* and *Ambrosia dumosa* in the study area, occur only along narrow channels or runnels. Annuals most commonly found on the pavement are *Phacelia neglecta*, *Chorizanthe rigida*, *Oligomeris linifolia*, and *Plantago fastigiata*.

Riverine dunes are low dunefields that occur infrequently on the floodplain adjacent to the Colorado River. Dunes have high rates of infiltration and consequently are relatively mesic habitats (Bowers 1982). Riverine dunes in the study area are dominated by *Atriplex canescens* subsp. *linearis* and *Tessaria sericea*. Some annuals that are common on dunes elsewhere in the Sonoran Desert region are found only on riverine dunes in the study area. These include *Dicoria*



FIGS. 2-5. Desert habitats of eastern Imperial Co., California. 2. North-facing slope in Cargo Muchacho Mountains, with sparse cover of *Encelia farinosa* and *Ambrosia dumosa*. 3. Gentle slopes (bajadas) south of Picacho Peak. The sparse cover in the foreground is mostly *Larrea tridentata*; *Cercidium floridum* and *Olneya tesota* line the wash in the midground. 4. Sandy flat south of Cargo Muchacho Mountains with *Encelia farinosa*, *Larrea tridentata*, and *Ambrosia dumosa*. 5. Ferguson Wash at southeast end of Chocolate Mountains; Ferguson Lake, Colorado River, and Martinez Lake in the background. Dense vegetation along wash includes *Cercidium floridum*, *Olneya tesota*, and *Condalia globosa*.

canescens, *Loeseliastrum schottii*, *Cryptantha costata*, *C. micrantha*, and *Phacelia pediculoides*.

Phytogeography. The study area is of interest to historical phytogeography because it is one of the few areas within the Southwest that remained a desert throughout the Wisconsin glaciation (Cole 1986). During the last ice age the vegetation and flora more closely resembled that occurring today in the Mohave Desert to the north. Species recorded from packrat middens found near Picacho Peak and dated to 13,000 yr B.P. include *Coleogyne ramosissima*, *Chrysothamnus teretifolius*, *Salvia mohavensis*, *Eriogonum fasciculatum*, *Brickellia atractyloides*, *Yucca brevifolia*, and *Yucca whipplei*, none of which occur in the modern flora. Species in the modern flora that were present in the oldest middens include *Larrea tridentata*, *Opuntia acanthocarpa*, *O. basilaris*, and *Ferocactus acanthodes*. Many of the modern dominants of the area, including *Ambrosia dumosa*, *Olneya tesota*, *Fouquieria splendens*, *Bebbia juncea*, *Ambrosia ili-*

cifolia, *Petalonyx linearis*, and *Fagonia laevis* do not appear in the fossil record until the last few thousand years.

Wetlands

The vegetation along the Colorado River has changed considerably during historical times. Doubtless there also have been undocumented changes in the flora. Extensive gallery forests of *Populus fremontii* and *Salix gooddingii* once lined both banks of the river (Grinnell 1914, Minckley and Rinne 1985). These gallery forests have been replaced by thickets of *Tamarix chinensis*, *Tessaria sericea*, *Salix exigua*, *Prosopis pubescens*, *Baccharis emoryi*, and *B. glutinosa* in the study area (Fig. 6). These thickets have been called "Sonoran riparian scrublands" by Minckley and Brown (1982).

Other important wetland habitats occurring along the river include sandbars, marshes, and alkaline depressions. Sandbars are inundated by the spring floods and exposed when water levels recede in the summer and fall. Older sandbars are dominated by *Salix exigua*, *Typha domingensis*, *Tamarix chinensis*, and other perennials; younger sandbars (Fig. 7) provide habitats for several annual and perennial species of *Cyperus*, *Eleocharis*, *Juncus*, and various Asteraceae. The marshes (Fig. 8) were described by Minckley and Brown (1982) and are dominated by several species of emergent perennials, including *Scirpus californicus*, *Typha domingensis*, and *Phragmites australis*, usually in dense, monospecific stands (Fig. 9).

The alkaline depressions form in fine-textured soils at the upper limit of spring floods (Grinnell 1914); dominant species include *Distichlis spicata*, *Suaeda moquinii*, and *Eustoma exaltatum*. Grinnell (1914) included *Allenrolfea occidentalis* as a dominant of such sites, but we have yet to encounter this widespread plant in the study area.

FLORA

The known vascular plant flora of the study area includes only 322 species (Table 2). Of these, 44 are introduced species, 12 are "native weeds" found mostly on disturbed sites (e.g., *Trianthema portulacastrum*, *Amaranthus palmeri*, *Conyza canadensis*, *Monolepis nuttalliana*, *Helianthus annuus*), and 56 species are found only in wetland habitats along the Colorado River. The flora of the undisturbed desert areas includes only 210 species. The low rainfall and moderate topographic relief within the study area probably account for the rather depauperate flora. Because of the extreme aridity, plant species do not "partition" the topographic gradient into several distinct habitats. Flats, washes, slopes, and mountain tops are uniformly unfavorable for much of the growing season for most of the



FIGS. 6-9. Wetland habitats of eastern Imperial Co., California. 6. Gallery forest remnant in Imperial National Wildlife Refuge. Trees are *Populus fremontii* and *Salix gooddingii*; dense thicket below trees along Colorado River includes *Phragmites australis*, *Tessaria sericea*, and *Tamarix chinensis*. 7. Recently formed sandbar in Colorado River, densely colonized by *Typha domingensis*. 8. Marsh at Picacho State Recreation Area with *Typha domingensis*. 9. Marsh with dense stand of *Scirpus californicus*.

flora. In other words, extreme aridity reduces habitat diversity, with a concomitant reduction in species diversity.

There are 15 genera within the study area with four or more species. *Camissonia* (7 spp.), *Cryptantha* (7 spp.), *Opuntia* (6 spp.), *Phacelia* (6 spp.), *Atriplex* (5 spp.), *Mentzelia* (5 spp.), *Astragalus* (4 spp.), and *Eriogonum* (4 spp.) are widespread and common throughout the Intermountain Southwest. *Chamaesyce* (5 spp.), *Lycium* (4 spp.), and *Aristida* (4 spp.) are well developed in the southern desert biogeographic provinces and *Scirpus* (5 spp.), *Cyperus* (4 spp.), *Eleocharis* (4 spp.), and *Juncus* (4 spp.) are widespread in warm temperate wetlands.

A tabulation of the flora by life-forms shows a high percentage of annuals and shrubs in the study area (Table 3). The absolute number of species of annuals and shrubs is probably no greater than would be expected on the basis of the size and elevational range of the study area (Bowers and McLaughlin 1982). This flora differs from more mesophytic southwestern floras in its low number of herbaceous perennials; annuals and shrubs are only *relatively* more abun-

TABLE 2. SUMMARY OF THE VASCULAR PLANT TAXA FOUND IN EASTERN IMPERIAL CO., CALIFORNIA, INCLUDING THE TEN LARGEST FAMILIES (LISTED IN DECREASING NUMBER, BY SPECIES).

Group	No. of families	No. of genera	No. of species	No. of non-natives
Vascular cryptogams	1	1	1	0
Gymnosperms	1	1	3	0
Dicotyledons	49	167	256	27
Monocotyledons	11	38	62	17
Total all groups	62	207	322	44
Asteraceae		41	48	2
Poaceae		25	32	14
Fabaceae		14	22	2
Boraginaceae		6	17	0
Cyperaceae		4	14	1
Chenopodiaceae		7	12	5
Polygonaceae		4	12	4
Solanaceae		6	12	2
Cactaceae		6	11	0
Euphorbiaceae		5	11	0

dant here due to the poor development of an herbaceous perennial flora. Only 50 species of perennial herbs occur in the undisturbed desert habitats, accounting for only 24% of the desert flora. In the more mesic wetlands of the Colorado River Valley, 35 herbaceous perennial species account for 63% of the species found only in wetland habitats on the study site. In the desert areas perennial herbs often are restricted to the relatively mesic microsites, i.e., steeper north-facing slopes and shaded banks of washes in deep sand.

ANNOTATED CATALOGUE

Botanical nomenclature follows Munz (1974), except where noted. Each species is annotated with notes on distribution and frequency. Frequency classes are: rare—known from only one or two localities or collections; infrequent—known from several localities, but found in only one or two habitats; occasional—often encountered, but found mostly in particular habitats; common—often encountered, occurring in several different habitats; and widespread—usually found in several different habitats. Collection numbers, except where noted, are for our collections deposited at ARIZ.

The catalogue is based primarily on our collections and field notes from 1983–1986. In addition, a list of species that are likely to occur in the study area was drawn up and the herbarium records at ARIZ, ASU, RSA, and SD were examined for collections of these species.

TABLE 3. GROWTH FORMS OF SPECIES FOUND IN EASTERN IMPERIAL CO. STUDY SITE AND THROUGHOUT THE SOUTHWESTERN UNITED STATES. ¹ Source: McLaughlin (1986).

Growth form	Percent of native species in:		
	Eastern Imperial Co.		Southwestern United States ¹
	Deserts	Wetlands	
Trees	2.4	7.1	4.3
Shrubs	21.9	5.4	14.8
Herbaceous perennials	23.8	62.5	53.0
Annuals	46.7	25.0	24.6
Succulents	5.2	0.0	3.3

Our emphasis was on the native, terrestrial species; aquatic and wetland habitats along the Colorado River were collected from several localities accessible by land and were more extensively examined by boat during the fall of 1986. Agricultural areas and other disturbed habitats were less intensively collected. Introduced species are preceded by an asterisk (*).

VASCULAR PLANTS OF EASTERN IMPERIAL COUNTY, CALIFORNIA

PTEROPHYTA

Pteridaceae

Notholaena parryi D. C. Eaton. Rare; n.-facing slopes, northwest end of Palo Verde Mtns.; 2897.

CONIFEROPHYTA

Ephedraceae

Ephedra aspera Engelm. Widespread; slopes and washes; 2762, 2893.

Ephedra fasciculata A. Nels. var. *clokeyi* (Cutler) Clokey. Occasional; slopes, Cargo Muchacho Mtns.; 2959.

Ephedra trifurca Torr. Rare; *Larrea* flats east of Midway Well; Wiggins 8552 (ARIZ).

ANTHOPHYTA—DICOTYLEDONEAE

Acanthaceae

Justicia californica (Benth.) D. Gibson [*Beloperone c.* Benth.]. Common; washes; 2802.

Aizoaceae

**Mesembryanthemum nodiflorum* L. [*Gasoul n.* (L.) Rotm.]. Occasional; alkaline depressions; 2632, 3242.

Trianthema portulacastrum L. Infrequent; fields and roadsides; 4138.

Amaranthaceae

Amaranthus palmeri S. Wats. Infrequent; fields and roadsides; 3054.

Tidestromia oblongifolia (S. Wats.) Standl. Common; flats and slopes; 2618, 2718.

Apiaceae

- Daucus pusillus* Michx. Rare; washes, west of Palo Verde Mtns.; 2880.
Hydrocotyle verticillata Thunb. Occasional; sandbars, banks of irrigation ditches; 3243, 3491.

Asclepiadaceae

- Asclepias albicans* S. Wats. Occasional; rocky slopes; 2934.
Asclepias erosa Torr. Rare; sandy wash near Midway Well; 3477.
Asclepias subulata Decne. Occasional; sandy flats; 3008.
Sarcostemma cynanchoides Decne. subsp. *hartwegii* (Vail) R. Holm. Occasional; washes, climbing in perennials; 2650.
Sarcostemma hirtellum (Gray) R. Holm. Occasional; washes; 2891, 2925.

Asteraceae

- Ambrosia dumosa* (Gray) Payne. Widespread; flats and all slopes; 3479.
Ambrosia ilicifolia (Gray) Payne. Occasional; washes and on n.-facing slopes about Picacho Peak; 2803.
Aster exilis Ell. Infrequent; sandbars; 3050.
Aster spinosus Benth. Infrequent; irrigation ditches and field borders; 3485.
Atrichoseris platyphylla Gray. Common; washes and gravelly slopes; 2647, 2811.
Baccharis emoryi Gray. Infrequent; sandbars, thickets, and marshes; 3055.
Baccharis glutinosa Pers. Common; sandbars and thickets; 3024, 3052.
Baileya pauciradiata Harv. & Gray. Infrequent; riverine dunes; 3224.
Baileya pleniradiata Harv. & Gray. Common; sandy flats and riverine dunes; 3026, 3134.
Bebbia juncea (Benth.) Greene. Common; washes; 3469.
Calycoseris wrightii Gray. Rare; rocky slopes and flats, Palo Verde Mtns.; 2902, 2926.
Chaenactis carphoclinia Gray. Common; slopes and washes; 2659, 2805.
Chaenactis stevioides Hook. & Arn. Common; slopes, washes, and riverine dunes; 2862, 2890, 3226.
Conyza canadensis (L.) Cronq. Infrequent; sandbars and disturbed sites; 3051.
Dicoria canescens Torr. & Gray. Rare; riverine dunes; Thornber, 22 Sep 1912 (ARIZ).
Dyssodia porophylloides Gray. Infrequent; slopes and canyons, Palo Verde Mtns.; 2914.
Eclipta alba (L.) Hassk. Rare; Colorado River, open water; Thornber 24 Sep 1912 (ARIZ), Pinkava et al. 10,358 (ASU).
Encelia farinosa Gray. Widespread; flats and mostly s.-facing slopes; 2759.
Encelia frutescens (Gray) Gray. Occasional; washes and on sandy flats near Ogilby Hills; 2904.
Geraea canescens Torr. & Gray. Widespread; flats, slopes, and desert pavement; 3473.
Gnaphalium purpureum L. Infrequent; sandbars and thickets; 3230.
Helianthus annuus L. subsp. *lenticularis* (Dougl.) Ckll. Infrequent; fields and roadsides; 2855, 3492.
Heterotheca sp. Occasional; sandbars; 3023, 4154, 4163, 4168.
Heterotheca subaxillaris (Lam.) Britt. & Rusby. Rare; sandbars north of Yuma; 3044.
Hymenoclea salsola Torr. & Gray. Common; washes; 2745.
Hymenoxys odorata DC. Infrequent; sandbars; Thornber 22 Sep 1912 (ARIZ), Ferris 22 Apr 1928 (RSA).
 **Lactuca serriola* L. Infrequent; disturbed ground; 3483.
Machaeranthera tephrodes (Gray) Greene. Infrequent; disturbed areas, roadsides; 3465.
Malacothrix glabrata Gray. Rare; rocky slopes, Palo Verde Mtns.; 2903.
Monoptilon bellioides (Gray) Hall. Widespread; washes, slopes, and flats; 2763, 2770.

- Palafoxia arida* B. L. Turner & M. I. Morris [*P. linearis* (Cav.) Lag.]. Common; sandy flats and riverine dunes; 2641, 2921, 3225.
- Pectis papposa* Harv. & Gray. Infrequent; sandy flats near Ogilby; 3060.
- Perityle emoryi* Torr. Widespread; washes, flats, and rocky slopes; 3470.
- Peucephyllum schottii* Gray. Common; mostly n.-facing, rocky slopes; 3487.
- Pleurocoronis plurisetia* (Gray) King & H. E. Robins. Common; n.-facing slopes; 2736.
- Pluchea odorata* (L.) Cass. [*P. purpurascens* (Sw.) DC.]. Common; sandbars and marshes; 2724, 3025.
- Porophyllum gracile* Benth. Occasional; slopes and flats; 2717, 2932.
- Prenanthes exigua* (Gray) Rydb. [*Stephanomeria e.* Nutt.]. Rare; rocky slopes, Palo Verde Mtns.; 2892.
- Psathyrotes ramosissima* (Torr.) Gray. Occasional; flats and slopes; 2636.
- Rafinesquia neomexicana* Gray. Common; washes and flats; rare on riverine dunes; 2863, 3223.
- Senecio mohavensis* Gray. Infrequent; washes and n.-facing slopes; 2773, 2904.
- **Sonchus oleraceus* L. Occasional; roadsides, fields, wasteground; 2730, 3229.
- Stephanomeria pauciflora* (Torr.) Nutt. Occasional; washes; 2642.
- Stylocline micropoides* Gray. Infrequent; gravelly flats; 2887, 2974.
- Tessaria sericea* (Nutt.) Shinners [*Pluchea s.* (Nutt.) Cov.]. Widespread; marshes, thickets, sandbars, and riverine dunes; 3011, 3498.
- Trichoptilium incisum* (Gray) Gray. Occasional; gravelly slopes and flats; 2630, 2912.
- Trixis californica* Kell. Common; n.-facing slopes; 3478.
- Xanthium strumarium* L. var. *canadense* (Mill.) Torr. & Gray. Rare; sandy banks; 4168B.

Bignoniaceae

- Chilopsis linearis* (Cav.) Sweet var. *arcuata* Fosb. Infrequent; washes; 2804.

Boraginaceae

- Amsinckia intermedia* Fisch. & Mey. Infrequent; washes, Palo Verde Mtns.; 2873.
- Amsinckia tessellata* Gray. Rare; n.-facing slope, Picacho Peak; 2798.
- Cryptantha angustifolia* (Torr.) Greene. Widespread; slopes, flats, washes, and riverine dunes; 2616, 2740, 2781.
- Cryptantha barbigera* (Gray) Greene. Occasional; sandy flats and washes; 2741, 2752, 2937.
- Cryptantha costata* Brandegees. Infrequent; riverine dunes; 3220.
- Cryptantha holoptera* (Gray) Macbr. Occasional; n.-facing slopes; 2734, 2737, 2789, 2799.
- Cryptantha maritima* (Greene) Greene. Common; sandy washes; 2631, 2739.
- Cryptantha micrantha* (Torr.) Johnst. Infrequent; riverine dunes; 3140.
- Cryptantha pterocarya* (Torr.) Greene. Infrequent; n.-facing slopes; 2788, 2962.
- Heliotropium curassavicum* L. var. *oculatum* (Heller) Jtn. Infrequent; alkaline depressions; 2818, 2972.
- Pectocarya heterocarpa* (Johnst.) Johnst. Common; washes, flats, and slopes; 2776.
- Pectocarya platycarpa* (Munz & Johnst.) Munz & Johnst. Common; rocky flats, washes; 2866.
- Pectocarya recurvata* Johnst. Rare; slopes; 2928.
- Plagiobothrys jonesii* Gray. Infrequent; sandy washes; 2782.
- Tiquilia canescens* (DC.) A. Richards. [*Coldenia c.* DC.]. Infrequent; volcanic slopes; 2760.
- Tiquilia palmeri* (Gray) A. Richards. [*Coldenia p.* Gray]. Occasional; sandy flats; 2640, 2711.
- Tiquilia plicata* (Torr.) A. Richards. [*Coldenia p.* (Torr.) Cov.]. Occasional; riverine dunes and other sandy soils; 2850.

Brassicaceae

- **Brassica tournefortii* Gouan. Common; sandy flats and washes, roadsides; 2742.
Caulanthus lasiophyllus (Hook. & Arn.) Payson [*Thelypodium l.* (Hook. & Arn.) Greene]. Widespread; flats and washes; 2778.
Descurainia pinnata (Walt.) Britt. subsp. *glabra* (Woot. & Standl) Detl. Rare; wash near Mitchell's Camp; 2923.
Dithyrea californica Harv. Common; sandy flats and riverine dunes; 2919, 3141.
Draba cuneifolia Nutt. var. *integrifolia* S. Wats. Infrequent; washes and n.-facing slopes, Palo Verde Mtns.; 2870.
Lepidium lasiocarpum Nutt. Common; washes; 2779, 2883, 3135.
Lesquerella palmeri S. Wats. Rare; 27 mi n. of Ogilby; Alexander and Kellogg 1924 (RSA).
 **Sisymbrium irio* L. Widespread; washes and disturbed areas; 2884.

Cactaceae

- Cereus giganteus* Engelm. [*Carnegiea g.* (Engelm.) Britt. & Rose]. Rare; several individuals vicinity of Senator Wash camp area, one plant near Ferguson Lake. Grinnell (1914) noted 75 plants on the California side of the Colorado River; there are many fewer today.
Coryphantha vivipara (Nutt.) Britt. & Rose var. *alversonii* (Coulter) L. Benson. Rare; mapped in study area by Benson (1982).
Echinocactus polycephalus Engelm. & Bigel. Occasional; rocky slopes, Chocolate Mtns.
Ferocactus acanthodes (Lem.) Britt. & Rose. Occasional; rocky slopes.
Mammillaria tetrancistra Engelm. Widespread; rocky slopes.
Opuntia acanthocarpa Engelm. & Bigel. var. *coloradensis* L. Benson. Occasional; gravelly flats and slopes near Colorado River.
Opuntia basilaris Engelm. & Bigel. Widespread; flats and slopes.
Opuntia bigelovii Engelm. Occasional; rocky slopes.
Opuntia echinocarpa Engelm. & Bigel. Common; slopes and flats, Palo Verde Mtns.
Opuntia ramosissima Engelm. Occasional; sandy and gravelly flats.
Opuntia wigginsii L. Benson. Infrequent; flats and slopes, Palo Verde Mtns.

Campanulaceae

- Nemacladus glanduliferus* Jepson. Common; washes and flats; 2775, 2813, 2910.
Nemacladus rubescens Greene var. *tenuis* McVaugh. Rare; 2 mi n. of Cargo Muchacho Mtns.; Munz and Hitchcock 12145 (RSA).

Caryophyllaceae

- Achryonichia cooperi* Torr. & Gray. Infrequent; sandy flats and washes; 2939, 3246.
 **Spergularia marina* (L.) Griseb. Infrequent; alkaline depressions; 2973, 3232.

Ceratophyllaceae

- Ceratophyllum demersum* L. Infrequent; Colorado River, open water; Ricci 10, Minckley and Dunfee YLD-32, YLD-54 (ASU).

Chenopodiaceae

- Atriplex canescens* (Pursh) Nutt. subsp. *linearis* (S. Wats.) Hall & Clem. Occasional; alkaline depressions and riverine dunes; 3027.
Atriplex elegans (Moq.) D. Dietr. subsp. *fasciculata* (S. Wats.) Hall & Clem. Occasional; desert pavement and roadsides; 2869, 3059.
Atriplex hymenelytra (Torr.) S. Wats. Occasional; rocky slopes, Chocolate Mtns.; 3481.
Atriplex lentiformis (Torr.) S. Wats. Common; alkaline depressions; 2777.

Atriplex polycarpa (Torr.) S. Wats. Common; washes; 2635B.

**Bassia hyssopifolia* (Pall.) Kuntze. Infrequent; roadsides, sandbars; 3094.

**Chenopodium album* L. Occasional; fields and roadsides; 3028.

**Chenopodium murale* L. Common; fields and roadsides; 2615, 2845.

**Kochia scoparia* (L.) Schrad. Occasional; fields and wasteground; 2949.

Monolepis nuttalliana (Schult.) Greene. Occasional; roadsides; 2954.

**Salsola australis* R. Br. [*S. iberica* Sennen & Pau]. Common; roadsides, wasteground, and riverine dunes; 3461.

Suaeda moquinii Greene [*S. torreyana* S. Wats. var. *ramosissima* (Standl.) Munz]. Common; washes and alkaline depressions; 3480.

Convolvulaceae

Cressa truxillensis HBK. Infrequent; alkaline depressions; *McMurray 1396* (ARIZ).

Cucurbitaceae

Brandegea bigelovii (S. Wats.) Cogn. Occasional; climbing in trees and shrubs, washes; 3476.

Cucurbita palmata S. Wats. Rare; near Bard; *Thorner 22 Sep 1912* (ARIZ).

Euphorbiaceae

Argythamnia lanceolata (Benth.) Muell.-Arg. [*Ditaxis l.* (Benth.) Pax & K. Hoffm.]. Common; washes and rocky slopes; 2746, 2755, 2758.

Argythamnia neomexicana Muell.-Arg. [*Ditaxis n.* (Muell.-Arg.) Heller]. Occasional; rocky slopes; 2613, 2738, 3061.

Argythamnia serrata (Torr.) Muell.-Arg. [*Ditaxis s.* (Torr.) Heller]. Infrequent; sandy flats; *Thorne et al. 50920* (RSA), *Balls and Everett 22900* (RSA).

Chamaesyce albomarginata (Torr. & Gray) Small. [*Euphorbia a.* Torr. & Gray]. Rare; Colorado River Valley; *Peirson 7200* (RSA).

Chamaesyce micromera (Boiss.) Woot. & Standl. [*Euphorbia m.* Boiss.]. Infrequent; sandy flats and washes; 2714, 3061.

Chamaesyce pediculifera (Engelm.) Rose & Standl. [*Euphorbia p.* Engelm.]. Occasional; rocky slopes, flats; 2915.

Chamaesyce polycarpa (Benth.) Millsp. var. *hirtella* (Boiss.) Millsp. [*Euphorbia p.* Benth. var. *h.* (Engelm.) Wheeler]. Widespread; washes and sandy and gravelly flats; 2614.

Chamaesyce setiloba (Engelm.) Millsp. [*Euphorbia s.* Engelm.]. Common; sandy washes and flats; 2719.

Croton californicus Muell.-Arg. var. *mohavensis* Ferg. Occasional; sandy flats; 2941.

Euphorbia eriantha Benth. Infrequent; washes; 2757, 2878.

Stillingia spinulosa Torr. Infrequent; sandy flats near Ogilby; *Balls and Everett 22899* (RSA), *Jones 8 May 1903* (RSA).

Fabaceae

Acacia greggii Gray. Common; washes; 2806.

Astragalus aridus Gray. Rare; found along the lower Colorado River Valley according to Barneby (1964).

Astragalus insularis Kell. var. *harwoodii* Munz & McBurney. Infrequent; sandy flats; 2942, 2946.

Astragalus lentiginosus Dougl. var. *borreganus* Jones. Rare; near Ogilby; *Balls and Everett 22896* (RSA), *Armstrong 1129* (SD).

Astragalus nuttallianus DC. var. *imperfectus* (Rydb.) Barneby. Rare; washes and sandy flats; 2886, 2943.

Caesalpinia virgata Fisher [*Hoffmannseggia microphylla* Torr.]. Infrequent; rocky slopes; 2909.

- Calliandra eriophylla* Benth. Occasional; washes and flats near Cargo Muchacho Mtns.; 2756, 2931.
- Cercidium floridum* Benth. Common; washes; 3468.
- Dalea mollis* Benth. Widespread; sandy and gravelly flats; 2715, 2776.
- Dalea mollissima* (Rydb.) Munz. Occasional; gravelly flats; 2733B, 2749.
- Lotus tomentellus* Greene. Occasional; washes and sandy flats; 2653, 2944, 3137.
- Lupinus arizonicus* (S. Wats.) S. Wats. Common; washes, flats, and slopes; 2645, 2814.
- Marina parryi* (Torr. & Gray) Barneby [*Dalea p.* Torr. & Gray]. Infrequent; washes and flats; 2898.
- **Melilotus albus* Desr. Infrequent; disturbed ground; 3460.
- **Melilotus indicus* (L.) All. Infrequent; roadsides, fields, irrigation ditches; 3247.
- Olneya tesota* Gray. Widespread; washes; 3472.
- Prosopis glandulosa* Torr. var. *torreyana* (L. Benson) M. C. Johnst. Occasional; broad washes; 3489.
- Prosopis pubescens* Benth. Infrequent; thickets along Colorado River; 2658.
- Psorothamnus emoryi* (Gray) Barneby [*Dalea e.* Gray]. Infrequent; sandy soils along Colorado River and Picacho Wash at All-American Canal; 2957, 3456. We have yet to find *Pilostyles thurberi* Gray on plants in our study area.
- Psorothamnus schottii* (Torr.) Barneby [*Dalea s.* Torr.]. Infrequent; washes; 2655.
- Psorothamnus spinosus* (Gray) Barneby [*Dalea s.* Gray]. Widespread; washes; 3474.
- Sesbania exaltata* (Raf.) Cory. Infrequent; sandbars, fields and irrigation ditches; 3047.

Fouquieriaceae

- Fouquieria splendens* Engelm. Widespread; desert pavement, flats, and rocky slopes.

Gentianaceae

- Eustoma exaltatum* (L.) Griseb. Infrequent; sandbars and alkaline depressions; 3016.

Geraniaceae

- **Erodium cicutarium* (L.) L'Her. Occasional; roadsides; 2917.
- Erodium texanum* Gray. Infrequent; gravelly flats and slopes; 2888.

Haloragaceae

- Myriophyllum exalbescens* Fern. Occasional; open water; 3042.

Hydrophyllaceae

- Eucrypta micrantha* (Torr.) Heller. Occasional; densely vegetated washes and n.-facing slopes; 2875, 2958.
- Nama demissum* Gray. Occasional; sandy washes; 2796.
- Nama hispidum* Gray var. *spatulatum* (Torr.) C. L. Hitchc. Occasional; sandy flats, washes; 2624, 2947.
- Phacelia ambigua* Jones var. *minutiflora* (Voss) Atwood [*P. minutiflora* J. Voss]. Common; washes, flats, and rocky slopes; 2810, 2872.
- Phacelia crenulata* Torr. Widespread; washes, flats, rocky slopes; 2651, 2868.
- Phacelia neglecta* Jones. Common; desert pavement, broad washes; 2795, 2868.
- Phacelia pachyphylla* Gray. Infrequent; slopes and washes; 2664, 3245.
- Phacelia pedicellata* Gray. Infrequent; rocky slopes; 2801.
- Phacelia pediculoides* (J. T. Howell) Constance. Rare; riverine dunes; 3138.

Krameriaceae

Krameria grayi Rose & Painter. Common; rocky slopes and flats; 2638.

Krameria parviflora Benth. var. *imparata* J. F. Macbr. Common; rocky slopes; *Thorne et al.* 50910 (RSA), *Ferris* 7172 (RSA).

Lamiaceae

Hyptis emoryi Torr. Common; broad washes and n.-facing slopes; 2743.

Salazaria mexicana Torr. Rare; n.-facing slopes, vicinity Picacho Peak; 2800, 2965.

Teucrium cubense L. Rare; Palo Verde Valley; *J. and L. Roos* 4201 (RSA), *Jepson* 5258 (RSA).

Loasaceae

Mentzelia affinis Greene. Rare; vicinity Cargo Muchacho Mtns.; *Peirson* 9791 (RSA), *Munz and Hitchcock* 12149 (RSA).

Mentzelia albicaulis (Hook.) Torr. & Gray. Infrequent; washes; 2874.

Mentzelia californica Thompson & Roberts. Rare; granitic flats east of Ogilby Hills; 2938.

Mentzelia involucrata S. Wats. Common; washes, flats, and rocky slopes; 2628.

Mentzelia longiloba J. Darl. Occasional; sandy flats, riverine dunes; 2955, 3136, 3227.

Petalonyx linearis Greene. Infrequent; rocky slopes; 2535, 2933.

Petalonyx thurberi Gray. Rare; 3 mi w. of Winterhaven; *Raven* 12909 (RSA), *McMinn* 1453 (RSA).

Lythraceae

Ammania coccinea Rottb. Rare; sandbars; *Irwin* 3 (ARIZ), *Thornber* 22 Sep 1912 (ARIZ).

Lythrum californicum Torr. & Gray. Infrequent; sandbars; 3019, 3045, 4165.

Malvaceae

Eremalche rotundifolia (Gray) Greene. Occasional; washes and gravelly flats; 2560, 2884.

Hibiscus denudatus Benth. Occasional; washes, flats, and slopes; 2716, 2754.

Horsfordia alata (S. Wats.) Gray. Rare; broad washes; 2750.

Horsfordia newberryi (S. Wats.) Gray. Rare; wash, Picacho State Rec. Area; 2732.

**Malva parviflora* L. Common; roadsides and fields.

Sida leprosa (Ort.) K. Schumm. var. *hederacea* K. Schumm. Infrequent; weed in cultivated areas; 4137.

Sphaeralcea ambigua Gray. Common; rocky slopes; 2720, 2960.

Sphaeralcea emoryi Torr. Occasional; sandy flats; 2968.

Martyniaceae

Proboscidea althaeifolia (Benth.) Decne. Rare; flats; *Thorne et al.* 50914 (RSA), *Stark* 1546 (RSA).

Nyctaginaceae

Abronia villosa S. Wats. Common; sandy flats, riverine dunes; 2945, 3142.

Allionia incarnata L. Common; rocky slopes; 3486.

Boerhaavia erecta L. var. *intermedia* (Jones) Kearney & Peebles. Infrequent; roadsides; 3058, 4144.

Boerhaavia triquetra S. Wats. Infrequent; washes and flats; 2734.

Boerhaavia wrightii Gray. Infrequent; washes, roadsides; 2725, 3056, 4143.
Mirabilis bigelovii Gray. Common; washes and n.-facing slopes; 2769, 2899.

Onagraceae

Camissonia arenaria (A. Nels.) Raven. Rare; rocky slopes; 2905.
Camissonia boothii (Dougl.) Raven subsp. *condensata* (Munz) Raven. Occasional; sandy flats; 2864, 2969.
Camissonia brevipes (Gray) Raven. Common; washes, flats; 2639, 2885, 2924.
Camissonia cardiophylla (Torr.) Raven. Common; rocky slopes, washes; 2619, 2787.
Camissonia chamaenerioides (Gray) Raven. Infrequent; washes and slopes; 2877, 2964.
Camissonia clavaeformis Torr. & Frem. subsp. *aurantiaca* (S. Wats.) Raven. Common; gravelly flats; 2876, 2889, 2970.
Camissonia refracta (S. Wats.) Raven. Common; washes and gravelly flats; 2646, 2816.
Oenothera deltoides Torr. & Frem. Infrequent; northeast side of Palo Verde Mtns.; Klein 144 (RSA).

Orobanchaceae

Orobanche cooperi (Gray) Heller. Infrequent; sandy and gravelly flats; Munz and Hitchcock 12152 (RSA), Balls and Everett 22927 (RSA).

Papaveraceae

Eschscholzia minutiflora S. Wats. Common; washes and flats; 2768.
Eschscholzia parishii Greene. Infrequent; flats n. of Cargo Muchacho Mtns.; 2927.

Pedaliaceae

**Sesamum indicum* L. Infrequent; cultivated in Colorado River Valley and occasionally found along roadsides; 4141.

Plantaginaceae

Plantago fastigiata Morris [*P. insularis* Eastw. var. *fastigiata* (Morris) Jeps.]. Widespread; slopes, flats, and washes; 2648.

Polemoniaceae

Gilia latifolia S. Wats. Infrequent; sandy washes; 2652.
Gilia stellata Heller. Widespread; washes, slopes, and flats; 2764, 2791, 2815, 2908.
Langloisia setosissima (Torr. & Gray) Greene. Occasional; washes, flats and slopes; 2649, 2817, 2911.
Linanthus jonesii (Gray) Greene. Occasional; washes and sandy flats; 2774, 2929.
Loeseliastrum schottii (Torr.) Timbrook [*Langloisia schottii* (Torr.) Greene]. Rare; riverine dunes; 2951, 3228.

Polygonaceae

Chorizanthe brevicornu Torr. Common; washes and flats; 2622, 2767.
Chorizanthe corrugata (Torr.) Torr. & Gray. Common; sandy and gravelly flats; 2629, 2871, 2936.
Chorizanthe rigida (Torr.) Torr. & Gray. Common; desert pavement, flats, and washes; 2623.
Eriogonum deflexum Torr. Common; washes and gravelly flats; 2621.
Eriogonum inflatum Torr. & Frem. Common; gravelly flats and slopes; 3467.
Eriogonum thomasi Torr. Widespread; washes, slopes, flats; 2625, 2657, 2857, 2867.

Eriogonum trichopes Torr. Infrequent; flats and gentle slopes; 2930.

**Polygonum argyrocoleon* Steud. Infrequent; alkaline depressions; 3234.

**Polygonum aviculare* L. Occasional; roadsides and wasteground; 2950.

Polygonum fusiforme Greene. Infrequent; marshes, canals, banks of Colorado River; 3236, 3248.

**Rumex conglomeratus* Murr. Infrequent; disturbed ground; 3493.

**Rumex persicarioides* L. Occasional; alkaline depressions and sandbars; 3015, 3235.

Portulacaceae

Calandrinia ambigua (S. Wats.) Howell. Infrequent; sandy flats; 2922.

Resedaceae

Oligomeris linifolia (Vahl) J. F. Macbr. Widespread; washes, desert pavement, sandy and gravelly slopes; 3463.

Rhamnaceae

Colubrina californica I. M. Johnst. Rare; Gavilan Wash e. of Indian Pass, Chocolate Mtns.; 2766.

Condalia globosa I. M. Johnst. var. *pubescens* I. M. Johnst. Common; broad washes and n.-facing slopes; 2858.

Zizyphus obtusifolia (Hook.) Gray [*Condaliopsis lycioides* (Gray) Suesseng var. *canescens* (Gray) Suesseng]. Occasional; n.-facing slopes; 3488.

Rubiaceae

Galium stellatum Kell. subsp. *eremicum* (Hilend & Howell) Ehrendf. Infrequent; n.-facing slopes, Palo Verde and Cargo Muchacho Mtns.; 2894, 2963.

Salicaceae

Populus fremontii S. Wats. Common; thickets and marshes; 3482.

Salix exigua Nutt. Occasional; sandbars; 3029, 3048.

Salix gooddingii Ball. Common; thickets and marshes; 2847.

Scrophulariaceae

**Bacopa monnieri* (L.) Wettst. Occasional; sandbars; 3239.

Mohavea confertiflora (Benth.) Heller. Common; washes, slopes, and flats; 2656, 2771.

Penstemon pseudospectabilis Jones. Infrequent; n.-facing slopes, Chocolate and Palo Verde Mtns.; 2784, 2913, 2969.

Simmondsiaceae

Simmondsia chinensis (Link) Schneider. Infrequent; sandy flats; 2748, 2901.

Solanaceae

Datura discolor Bernh. Occasional; washes; 2712.

Lycium andersonii Gray. Common; washes and n.-facing slopes; 2633, 2747, 2786, 2845.

Lycium fremontii Gray. Infrequent; washes; 2807.

Lycium parishii Gray. Infrequent; washes, Palo Verde Mtns.; 2879.

Lycium torreyi Gray. Infrequent; sandy flats and washes near Colorado River; 2643, 2952.

**Nicotiana glauca* Grah. Infrequent; along drainage ditches; 3496.

Nicotiana trigonophylla Dunal. Common; washes and n.-facing slopes; 2654.

Petunia parviflora Juss. Infrequent; sandbars; *Swingle* 260 (ARIZ), *Monson* 11 (ARIZ), *Parish* 8322 (RSA).

Physalis acutifolia (Miers) Sandwith. Infrequent; weed of agricultural areas; 4139.

Physalis angulata L. var. *lanceolata* (Nees) Waterfall. Infrequent; weed of agricultural areas; 4140.

Physalis crassifolia Benth. var. *versicolor* (Rydb.) Waterfall. Occasional; washes, flats, and slopes; 2728, 2751, 2753.

**Solanum elaeagnifolium* Cav. Infrequent; roadsides and fields; 3053.

Tamaricaceae

**Tamarix chinensis* Lour. Common; marshes and thickets; 2634, 3030.

**Tamarix ramosissima* Ledeb. Occasional; washes, ditches, and alkaline depressions; 2794.

Urticaceae

Parietaria floridana Nutt. Rare; rocky, n.-facing slopes, Picacho Peak and vicinity, Chocolate Mtns.; 2797, 2966.

Viscaceae

Phoradendron californicum Nutt. Common; in *Olneya*, *Prosopis*, and *Acacia*; 3475.

Zygophyllaceae

Fagonia laevis Standl. Common; mostly on rocky slopes; 2617.

Fagonia pachyacantha Rydb. Infrequent; slopes, Picacho State Rec. Area; 2627.

Larrea tridentata (DC.) Coville. Widespread; sandy and gravelly slopes, washes, and steep rocky slopes; 2744.

**Tribulus terrestris* L. Occasional; roadsides, disturbed areas; 3009.

ANTHOPHYTA—MONOCOTYLEDONEAE

Alismataceae

Echinodorus berteroi (Spreng.) Fassett. Rare; marshes; *Monson* 2 (ARIZ).

Araceae

**Pistia stratiotes* L. Rare; drainage canal, Ft. Yuma; *Peebles and Noble*, 28 Oct 1941 (ARIZ).

Cyperaceae

**Cyperus alternifolius* L. Infrequent; sandbars near Yuma; 3014.

Cyperus erythrorhizos Muhl. Occasional; sandbars; 3012, 3022.

Cyperus laevigatus L. Infrequent; sandbars; 3241.

Cyperus odoratus L. Common; sandbars and marshes; 2852, 4134.

Eleocharis coloradoensis (Britt.) Gilly. Infrequent; sandbars; 4150.

Eleocharis geniculata (L.) Roemer & Schultes. Common; sandbars, marshes and thickets; 2851, 2860, 3497.

Eleocharis macrostachya Britton in Small. Rare; sandbars; *Thornber* 24 Sep 1912 (ARIZ).

Eleocharis parishii Britt. Infrequent; sandbars; 4153.

Fimbristylis vahlII (Lam.) Link. Infrequent; sandbars; *Parish* 8375 (RSA), *Thornber* 25 Sep 1912 (ARIZ).

Scirpus acutus Muhl. Rare; marshes; *Striegler* 20 (ARIZ), *Behrends* 1 (ASU).

Scirpus americanus Pers. Occasional; sandbars and marshes; 3240, 3244.

Scirpus californicus (C. A. Mey.) Steud. Common; marshes; 2859, 3020.

Scirpus robustus Pursh. Infrequent; sandbars and marshes; *Goodding 43-1* (ARIZ), *McMurray 1397* (ARIZ).

Scirpus validus Vahl. Infrequent; marshes; *Booth A-112* (ARIZ), *McMurray 1365* (ARIZ).

Juncaceae

Juncus acutus L. var. *sphaerocarpus* Engelm. Infrequent; sandbars; 3045, 3237, 3490.

Juncus articulatus L. Rare; sandbars; 4161.

Juncus bufonius L. Rare; sandbars; *Peebles and Harrison 5062* (ARIZ), *Griner 10 Mar 1941* (ARIZ).

Juncus torreyi Cov. Occasional; sandbars; 3020, 4147.

Lemnaceae

Lemna gibba L. Rare; drainage ditches; 3233, 3501.

Liliaceae

Hesperocallis undulata Gray. Occasional; sandy and gravelly flats; 2920.

Najadaceae

Najas marina L. Infrequent; Colorado River backwaters; 4159.

Poaceae

Aristida adscensionis L. Widespread; slopes, flats, and washes; 2637.

Aristida californica Thurb. Infrequent; riverine dunes and sandy flats; 3462.

Aristida purpurea Nutt. Occasional; slopes; 2906.

Aristida wrightii Nash. Occasional; slopes; 2846, 2895.

**Avena fatua* L. Common; fields and roadsides; 2856.

Bouteloua aristidoides (HBK.) Griseb. Common; sandy flats and washes; 2721.

Bouteloua barbata Lag. Infrequent; sandy and gravelly flats; 2722.

**Bromus catharticus* Vahl [*B. willdenowii* Kunth]. Infrequent; roadsides and waste-ground; 3238.

**Cynodon dactylon* (L.) Pers. Common; fields and roadsides.

Diplachne uninervia (Presl) Parodi [*Leptochloa u.* (Presl) Hitchc. & Chase]. Occasional; alkaline depressions and sandbars; 2723, 3231.

Distichlis spicata (L.) Greene var. *stricta* (Torr.) Beetle. Infrequent; alkaline depressions; 2971.

**Echinochloa colonum* (L.) Link. Infrequent; sandbars near Yuma; 3017.

Eragrostis pectinacea (Michx.) Nees. Infrequent; alkaline depressions; 2854.

Eriochloa aristata Vasey. Rare; near Bard; *Reeder 29 Jun 1944* (ARIZ).

Erioneuron pulchellum (HBK.) Tateoko. Occasional; slopes and flats; 2865.

Heteropogon contortus (L.) Beauv. Rare; wash, w. side of Palo Verde Mtns.; *Fuller 19014* (RSA).

Hilaria rigida (Thurb.) Benth. Common; washes and n.-facing slopes; 2713.

**Hordeum glaucum* Steud. Occasional; roadsides; 2916.

**Hordeum vulgare* L. Occasional; roadsides, sandy flats; 2918.

**Leptochloa filiformis* (Lam.) Beauv. Infrequent; weed in agricultural areas; 4142.

Muhlenbergia microsperma (DC.) Kunth. Common; washes; 2731, 2882.

**Paspalum dilatatum* Poir. Rare; disturbed ground; 3503.

Paspalum distichum L. Rare; irrigation ditch; *Goodding and Reeder 8 Sep 1943* (ASU).

**Pennisetum setaceum* (Forsk.) Chiov. Rare; roadside near Laguna Dam; 2849.

**Phalaris minor* Retz. Occasional; fields and roadsides; 2948.

Phragmites australis (Cav.) Trin. Widespread; marshes and sandbars; 2953, 4158.

**Polypogon monspeliensis* (L.) Desf. Occasional; irrigation and drainage ditches; 2853, 3494.

- **Schismus barbatus* (L.) Thell. Common; flats and washes; 2761.
 **Sorghum bicolor* Moench. Infrequent; roadsides; *Barr* 66-39 (ARIZ).
 **Sorghum halepense* (L.) Pers. Infrequent; fields and wasteground; 4135.
Tridens muticus (Torr.) Nash. Rare; n.-facing slopes, Palo Verde Mtns.; 2896.
Vulpia octoflora Rydb. [*Festuca o.* Walt.]. Occasional; washes; 2784.

Potamogetonaceae

- **Potamogeton crispus* L. Common; shallow water in Colorado River; 4146.
Potamogeton foliosus Raf. Infrequent; Colorado River; 4160.
Potamogeton nodosus Poir. Rare; Colorado River; *Monson* 3 (ARIZ).
Potamogeton pectinatus L. Common; Colorado River; 3502, 4145.

Typhaceae

- Typha angustifolia* L. Infrequent; marshes; *Tuttle* 14 Sep 1959 (ARIZ).
Typha domingensis Pers. Common; marshes; 3459.

Zannichelliaceae

- Zannichellia palustris* L. Occasional; drainage ditches and sandbars; 3500, 4148.

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NOTES

THE RANGE AND TWO NEW LOCATIONS OF *Boschniakia strobilacea* (OROBANCHACEAE).—The known range of the root parasite *Boschniakia strobilacea* Gray (Ground Cone) is from Vancouver Island, B.C., Canada [1885, *Macoun s.n.* (GH)] south to the San Jacinto Mountains, Riverside Co., California [Reed 2535 (JEPS)]. A gap in this range has existed between San Benito Peak, San Benito Co. [Jepson 2718 (JEPS)] and Mt. Williamson, San Gabriel Mountains, Los Angeles Co. [9 Nov 1968, *Thorne et al. s.n.* (RSA)], a distance of 330 km.

Two recent collections have narrowed this gap: one in the Scodie Mountains, Kern Co. [3 Jul 1984, *Shevock 10948* (RSA, CAS)] and another on Dry Lakes Ridge, Ventura Co. [Magney 195-83, 124-84, 31-86, 32-86 (UCSB)]. The latter collections were reported recently by Magney (A flora of Dry Lakes Ridge, Ventura Co., UCSB Herb. Publ. No. 5, 1986). The Scodie Mountains locality is approximately 100 km north of the Mt. Williamson site and 245 km southeast of the San Benito Peak population. The Dry Lakes Ridge site is 130 km west of Mt. Williamson, 235 km south of San Benito Peak, and 170 km southwest of the Scodie Mountains (Fig. 1, page 380).

Boschniakia strobilacea is a fleshy-stemmed, parasitic herb 15–25 cm tall that arises from a corm-like thickening at the junction with the root of the host plant (Gilkey, Oregon St. Monogr., Studies in Botany No. 9, 1945). The leaves are scalelike, mostly imbricated, and brownish. The flowers are dark reddish-brown and occur on a thick spike 3.5–6 cm thick. Flowering occurs from April through July. *Boschniakia strobilacea* grows in a wide range of plant communities from near sea level to 2277 m in the northern portion of its range, and from 1450 m at Dry Lakes Ridge (Magney, op. cit.) to over 3015 m in southern California (Munz, A California fl., 1959; Abrams and Ferris, Illustr. fl. Pacific States, 1960). Gray (Pacific Railroad Report iv, 118 (1857), 1876) described it from a specimen collected in the foothills of the Sierra Nevada. Label data from the type specimen reads, “dry and rocky hills, South Yuba, California” [23 May 1854, *Bigelow s.n.* (NY)].

Specimen label data obtained from many herbaria (A, CAS, CSUC, DAV, F, GH, HSC, JEPS, K, LA, NY, RSA, SD, SFSU, UC, UCR, UCSB, US) indicate that *B. strobilacea* has been collected most frequently in northern California. Approximately 300 collections are from about 150 locations throughout its range (Fig. 1). A list of collection sites obtained from the herbaria mentioned above is available from the author upon request.

Arbutus menziesii and *Arctostaphylos glauca*, *A. nevadensis*, *A. parryana*, *A. patula*, *A. pungens*, and *A. tomentosa* have been suggested as host plants for *B. strobilacea*. The Dry Lakes Ridge population adds another host, *Arctostaphylos glandulosa*.

I appreciate the comments of reviewers L. Heckard, C. Mason, B. Tanowitz, an anonymous reviewer, and the editor.—DAVID L. MAGNEY, Dames & Moore, 175 Cremona Dr., Suite A-E, Goleta, CA 93117. (Received 17 Dec 1986; revision accepted 15 Jul 1987.)

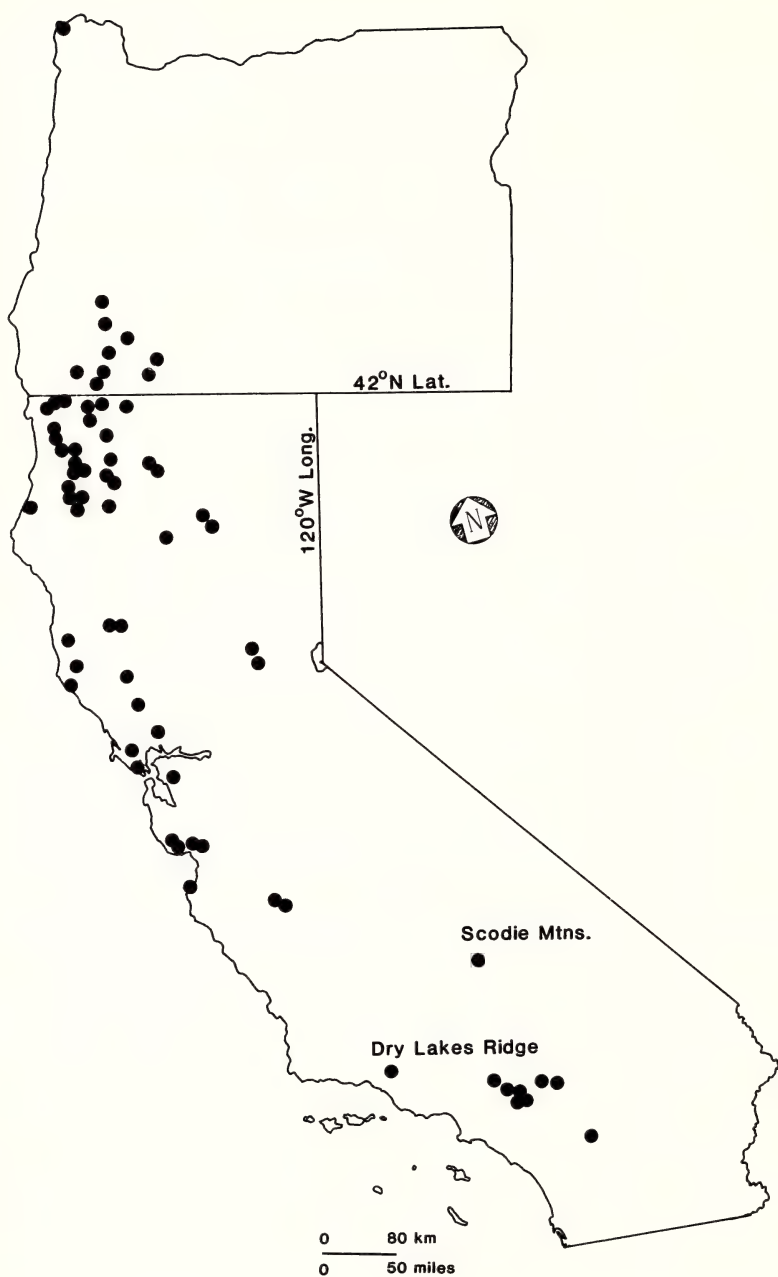


FIG. 1. Distribution of *Boschniakia strobilacea* Gray in California and Oregon. It also has been collected from Vancouver Island, B.C., Canada (not shown). ● = one or more collections of *B. strobilacea* and roughly represents one population.

NOTEWORTHY COLLECTIONS

CALIFORNIA

SCRIBNERIA BOLANDERI (Thurb.) Hack. (POACEAE).—San Diego Co., Del Mar Mesa, Caltrans vernal pool preserve, at the edges of vernal pools with *Agrostis microphylla*, *Festuca myuros*, *Juncus bufonius*, etc. in an area of *Adenostoma chaparral*, T14S R3W S23, 128 m, 28 Apr 1987, Moran, Rilling, and Zedler s.n. (SD).

Significance. Fills a gap between California collections from Santa Barbara Co., ca. 340 km nw. (Smith, A Flora of the Santa Barbara Region, CA, 1976), and Kern Co., ca. 320 km n. (Twissleman, A Flora of Kern County California, 1967); and the single Mexican collection from Laguna Hanson, Baja California Norte, ca. 160 km se. (R. F. Thorne, RSA, pers. comm.).

AGROSTIS AVENACEA Gmel. (POACEAE).—San Diego Co., Kearny Mesa, Miramar Mounds National Landmark, Miramar Naval Air Station, ca. 100 m w. of Hwy. 163 and 50 m n. of the as yet uncompleted extension of Hwy. 52, 32°50'30"N, 117°8'00"W, 130 m. In an artificially impounded seasonal wetland with *Polypogon monspeliensis*, *Eleocharis acicularis*, *E. cf. macrostachya*, *Aponogeton distachyus*, and a variety of native vernal pool species, 7 Jun 1987, Zedler, Moran, and Rilling s.n. (SD).

Significance. First report of this introduced species from southern California. Like *Aponogeton* (Keeley and Keeley, Madroño 26:188, 1979), this species may have invaded because of the unusually long water duration imposed on a former vernal pool area by the highway blocking the drainage. Known previously from n. CA (Crampton, Grasses in CA, 1974) and scattered locations in central U.S.; native to Australia, New Zealand, and the South Pacific.—PAUL H. ZEDLER, VIRGINIA MORAN, TRUDY RILLING, Biology Dept., San Diego State Univ., San Diego, CA 92182-0057; and GEOFFREY A. LEVIN, Botany Dept., San Diego Natural History Museum, P.O. Box 1390, San Diego, CA 92112-1390.

PETERIA THOMPSONAE S. Wats. (FABACEAE).—Inyo Co., Kingston Range, California Valley, Mesquite Valley Rd. 8 mi ne. of Smith Talc Mine Rd., sandy bajada, 2700 ft, 4 May 1980, de Nevers 150 (RSA).

Significance. First report of genus from California. Previously known from adjacent Nye and Clark cos. in NV.—AARON LISTON, Rancho Santa Ana Botanic Garden, Claremont 91711.

ECUADOR

BUDDLEJA AMERICANA L. (BUDDLEJACEAE).—Ecuador, Galapagos Islands, Floreana, Cerro de Naranjas, 200 m, 13 Feb 1986, J. E. Lawesson and H. Zederhof 2849 (CDS, DLF, QCA); e. of Cerro Pajas, near Wittmer's farm, 13 Feb 1986, Y. Carvajal 162 (CDS). Several hundred plants of several ages observed, associated with common guava in the first location and with a *Scalesia pedunculata* forest in the latter.

Previous knowledge. Floreana, near Wittmer's farm, 330 m, 14 Mar 1970, S. Itow 31400-1 (DS), but unreported previously. Known from Mexico to Bolivia, Cuba, and Jamaica (Norman, Buddlejaceae, Fl. Ecuador, 1982).

Significance. New family for the Galapagos Islands. Older settlers report (F. Cruz, pers. comm.) it was present 50 years ago.—ELIANE M. NORMAN, Dept. Biology, Stetson Univ., DeLand, FL 32720; and JONAS E. LAWESSON, Estacion Cientifica Charles Darwin, Isla Santa Cruz, Galapagos, Ecuador. Field work was supported by Danish

Natural Science Council, grants 11-5471 and 11-5663 to JEL. We are grateful to the Galapagos National Park Service and Charles Darwin Research Station for their assistance.

NEVADA

ASTRAGALUS GILMANII Tidest. (FABACEAE).—Lincoln Co., Groom Mountain Range, ca. 110 km w. of Caliente, occasional on tuff, se. side of basalt cone just n. of Cattle Spring in scattered Pinyon-Juniper, T6S R55½E S18, 1830 m, 7 May 1985, *Marrs-Smith and Nachlinger 91* (NY, RENO, UNLV) (determined by R. C. Barneby, NY).

Significance. First record for NV and an e. range extension of ca. 215 km from the Panamint Mtns., Inyo Co., CA.

ERIGERON OVINUS Cronquist (ASTERACEAE).—Lincoln Co., Groom Mountain Range, ca. 110 km w. of Caliente, limestone ridge with *Cercocarpus ledifolius* and *Forsellesia nevadensis*, T7S R56E S6, 2260 m, 4 Jun 1985, *Marrs-Smith and Nachlinger 47* (NY, RENO, UNLV).

Significance. A w. range extension of 29 km. Known only from Clark and Lincoln cos., NV.

POLYGALA SUBSPINOSA S. Wats. var. *HETERORHYNCHA* Barneby (POLYGALACEAE).—Lincoln Co., Groom Mountain Range, ca. 110 km w. of Caliente, on volcanic tuff with scattered *Artemisia tridentata*, T6S R55E S13, 1890 m, 7 May 1985, *Marrs-Smith s.n.* (NY) (determined by R. C. Barneby, NY).

Significance. First record for Lincoln Co. and a n. extension of ca. 60 km. Previously known from Clark and Nye cos., NV.—GAYLE MARRS-SMITH, Dept. Biological Sciences, Univ. Nevada, Las Vegas, 89154; and JAN NACHLINGER, Biological Sciences Center, Desert Research Inst., Reno, NV 89506.

REVIEW

Poisonous Plants of California. By THOMAS C. FULLER and ELIZABETH MCCLINTOCK. 433 pp. + 16 color plates. University of California Press, Berkeley, CA.

This volume is one of the California Natural History Guides (#53) published by the U.C. Press. This interesting and readable book provides a broad overview of plant toxicity at an introductory level. The main body consists of brief descriptions of hundreds of plants and fungi poisonous to humans and animals. It includes brief descriptions of symptoms of poisonings, brief chemical identification of the toxins, and interesting anecdotes of poisoning case histories. Included also are several useful species lists such as the most seriously poisonous plants and fungi, plants most often toxic to livestock, plants causing dermatitis, plants causing hay fever and plants accumulating nitrates. Although most of the book deals with flowering plants, there are also brief chapters on toxic algae, fungi, ferns and horsetails, and gymnosperms. The flowering plants are treated alphabetically by family. The book is well organized and cross referenced so as to facilitate finding specific information about plants or toxins. There are separate indices of common and scientific names, as well as a general subject index. There are many (but not enough) good line illustrations, and over 60 small but very good color photos that stress diagnostic characteristics.

There is a separate chapter on the chemistry of plant toxins and derivative drugs which is written in non-technical terms understandable to the layperson. The basic chemistry of allelopathy and photosensitization are described briefly. The reader with more knowledge of plant chemistry, especially of secondary metabolites, will be tantalized continually and will want to dig back into the literature for more detailed information.

This book contains no identification keys, but provides an excellent starting place to learn about both California native and introduced toxic plants. Although the descriptions of the plants are brief and non-technical, they are accurate and stress the diagnostic characteristics. There is no attempt to duplicate the exhaustive, botanically complete plant descriptions and keys as in Munz's *California Flora* and Bailey's *Manual of Cultivated Plants*. Likewise, because the descriptions of the chemistry and symptoms of toxicity are very brief, and considering the omission of antidotes and medical treatments, it can be concluded that medical advisement is prudently beyond the scope of the book. The book will be able to provide a quick, preliminary identification of plant material, toxins, and symptoms.

Poisonous Plants of California is welcome due to the on-going interest in diet, health, herbs, and edible and medicinal plants. I will put this book on my shelf next to the mushroom identification books and alongside Lewis' *Medical Botany* and Lampke's *Plant Toxicity and Dermatitis*. As a botany teacher, I am often asked by students about the toxicity (edibility, caffeine content, medicinal use, etc.) of some particular plant (mushroom, weed, herb, ornamental, etc.). It will be the first book I pull off my shelf to answer those questions. This book will be useful to anyone with an interest in plant edibility, toxicity, or medicinal qualities. It will be especially useful to naturalists, field biologists, ranchers, emergency room physicians, and veterinarians.—ROBERT CUMMINGS, Dept. Biological Sciences, Santa Barbara City College, Santa Barbara, CA 93109.

ANNOUNCEMENT

CORRECTIONS TO CBS SPEAKER SCHEDULE* FOR 1987-1988

<u>Date</u>	<u>Speaker & Topic</u>
Jan 21	Donald Koehler, Santa Barbara "Spectral quality of yellow flowers in relation to pol- lination"
Feb 20	Stephen J. Gould Annual Banquet, Topic to be announced
May 19	Meeting room at UC Botanic Garden, not LSB 2503

* See Madroño 34(3):272.

LETTERS

Dear Editor:

I'd like to give a rather general response to the request for reviewer's opinions on the amount of interest each paper might stimulate among the members of the California Botanical Society. I occasionally review manuscripts for *Madroño* and I am interested in new species descriptions. In general, such papers aren't too exciting. Nevertheless, they constitute a significant aspect of systematics and I think *Madroño* should continue to provide a place for such papers, especially when they deal with California taxa. Perhaps more important for CBS's general membership, however, is the role that new species descriptions have for environmentalists. For example, in some papers, the new species is judged by authorities to have a highly restricted range. This information may be quite valuable in future efforts to protect land where the new species grows. Furthermore, brief accounts on how new species were "discovered" also can be exciting illustrations of how interested amateurs can be involved in furthering scientific knowledge of our native flora. Thus, it might be good to actually encourage authors of new species descriptions to include people-oriented and environmental information!

Mark A. Schlessman
Dept. of Biology
Vassar College
Poughkeepsie, NY 12601

COMMENTARY

MESSAGE FROM THE PAST CBS PRESIDENT

It is with great pleasure that I address the membership of the California Botanical Society in this message column that was initiated at the suggestion of Wayne Ferren in our October 1986 issue of *Madroño*.

For decades, our journal has served as the vital organ for disseminating the results of scientific research to our membership. Historical convention and space limitations have all too often precluded commentaries that encourage dialogue or summarize the Society's activities, accomplishments, and aspirations for the future. Due in large part to Ferren's efforts, this is changing in a positive way. In conveying information on the inner workings of our Society, it is my hope that this column will help to serve as a catalyst for more communication and constructive input from our members.

The By-Laws of CBS give us a broad mandate—"... to stimulate interest and to further advancement in the entire field of botany especially in the western United States". This charge has rested largely on the shoulders of a cadre of elected and appointed volunteers, the Executive Council, who meet at Berkeley on a monthly basis during the academic year to formulate policy, tend to routine business, and plan for the future. The Council addressed a heavy agenda during the past year. The burdensome task of handling the Society's financial transactions and modest investments required careful consideration. The heavy demands on the CBS Treasurer led to the creation of the new position of Financial Officer. Our incumbent Treasurer, Dr. Cherie L. Wetzel, kindly agreed to continue her long service to the Society by assuming the duties of this new position, and Dr. Thomas F. Daniel accepted an appointment to the Council as our new Treasurer. These changes also forced us to take a closer look at the Society's financial health. The Society's major financial commitment each year is the publication of *Madroño*. Printing costs, however, have escalated an estimated 30% during the last six years. During this time, we have held to a steadfast policy of no dues increases because the Council strongly believed in providing its members with a quality journal at a bargain basement price. We will

continue to produce a journal of the quality that we currently enjoy, but we can do so only by implementing modest dues increases that will go into effect with volume 35 of *Madroño*. For the short term, this will put us in a sound financial position that will allow us to continue to provide partial support for worthy scientific endeavors. We continue to support the annual CBS Graduate Student Meetings and provide small cash awards for the best papers in several categories. Year before last we made a much-needed contribution toward the start-up phase of the Jepson Herbarium revision of the "Manual of the Flora of California". This past year we provided a modest no-interest loan that together with financial assistance from the California Native Plant Society will facilitate the publication of a new edition of "Terrestrial Vegetation of California". During the past year, the Council directed its attention to some projects that were deemed long overdue. Council member Barbara Ertter spearheaded the drive to assemble a computerized questionnaire that will be used to produce the Society's first membership directory. We have also explored the possibilities of publishing a comprehensive cumulative index to all published volumes of *Madroño*. The latter project could prove to be more costly than initially anticipated, but some decision on the most cost-effective method of producing an index should be reached during the coming year. To comfortably support the above kinds of projects on an ongoing basis, it will be imperative that the Society enhance its income base. This could be accomplished by a vigorous membership drive and perhaps the solicitation of private and corporate support. This must all be done in a way that will not jeopardize our non-profit, tax exempt status.

The most onerous task that confronted the Council during the past year was the selection of a new Editor to succeed Wayne Ferren who will complete his term early in 1988. Only the job of Editor itself exceeds the task of identifying a talented and qualified individual willing to give freely of his or her time in the service of science. I am pleased to announce that Dr. David J. Keil accepted our invitation to become the new Editor of *Madroño*. The Council joins me in welcoming him aboard. We regret that Wayne's term has passed so swiftly. He assumed his editorial duties with alacrity and good humor during a difficult transition period. He has maintained a standard of excellence and introduced new and effective format changes that we will want to continue. Our thanks to you, Wayne, for a job well done! We look forward to your continued advice as a member of the Board of Editors.

In reviewing Society activities, I note with concern a total lack of graduate student response to the financial support offered by the Society in the form of small research grants to assist with field work, travel expenses, and supplies. I encourage all interested students and/or their advisors to contact the CBS President for more information on this potential source of research support.

In closing I would like to thank our Executive Council, our Editor, Associate Editor, and their Board, and the many reviewers who have graciously given of their time and expertise during the past year. I would be remiss if I neglected to extend our appreciation to the diverse group of scientists who continue to share their observations and research findings with us through the printed pages of *Madroño*. —FRANK ALMEDA, Dept. Botany, California Academy of Sciences, Golden Gate Park, San Francisco, CA 94118-9961.

EDITOR'S REPORT FOR VOLUME 34

This annual report provides an opportunity for the Editor to communicate the status of manuscripts received for publication in *Madroño* and to comment on other aspects of the journal. Between 1 Jul 1986 and 30 Jun 1987, 80 manuscripts were received (37 articles, five notes, 38 individual noteworthy collections). Since 30 Jun 1987, 18 manuscripts (8, 1, 9) have been received. The current status of the 93

unpublished manuscripts is 26 in review (13, 2, 11), 28 in revision (25, 3, 0), eight needing a decision by the editors (6, 2, 0), and 31 accepted for publication (9, 1, 21). There are two unpublished book reviews. Volume 34 included 81 published manuscripts (32, 2, 35), nine book reviews, and three commentaries or letters. The period between submittal and publication averaged 1.5 years for articles. We rejected five manuscripts in 1987, and one was withdrawn by the author.

With publication of this issue, I complete my term as Editor of *Madroño*. I am honored to have served the California Botanical Society in this capacity and I hope my editorship has contributed to the growth of this important regional journal. The success of the past year is shared with many individuals who have helped guide *Madroño* and its editor. Marion Cave provided photographs for the dedication; Barry D. Tanowitz, Associate Editor, provided much editorial and technical advice and often sparked healthy debate on many topics; Steven Timbrook, member of the Board of Editors, contributed the Table of Contents and the Index to volume 34, a job appreciated by all members and subscribers. Thanks Barry and Steve! I also give special thanks to Annetta Carter, who has been a mentor during my editorship.

I thank the Executive Council of CBS for its guidance and the Board of Editors and the numerous reviewers (62) for their assistance with volume 34. Many reviewers, e.g., Jim Henrickson, Mary Carroll, Bill Critchfield, Susan Conard, and John Strother, commented on several of the manuscripts published this year and I am grateful for their dedication to *Madroño*. The organization, readability, and style of all papers reflect ideas provided by our reviewers and the high quality of papers in *Madroño* is attributed in part to their sincere efforts. In addition, the excellent style, clarity, and general appearance of our journal is always enhanced by the exceptional assistance provided by my friends at Allen Press.

During the past 2.5 years as Editor, I have implemented several policies that I hope will continue to stimulate interaction among members of the Society and the readership of our journal. Editorials, commentaries, letters to the editor, and announcements have extended our journal beyond its role as a vehicle for reporting science to one also of comment and reflection. With the publication of 35(1), *Madroño* also will be a bilingual journal. Members of the CBS have a long-term and increasing interest in the flora and vegetation of Mexico and Central and South America. Because of this interest, I believe our new policy to publish Spanish language papers with English abstracts and, where appropriate, English language papers with Spanish abstracts will open *Madroño* to an even wider readership, perhaps increase the membership in CBS, and extend a gesture of goodwill to our Hispanic colleagues and neighbors. There has been widespread support for this decision, and I request that all members encourage their Hispanic colleagues to join the CBS and contribute to *Madroño*. I thank Roberto Iglesias Prieto (UCSB) and various reviewers for assistance with these manuscripts, and David J. Keil (the new Editor) for his encouragement.

Most important to *Madroño*, however, are the contributions by authors. The strength of our journal depends on the quality and quantity of manuscripts, and a review of papers published in volume 34 reveals the diversity of botanical investigations reported by members of the Society. For example, we have published contributions in historical botany, ecology, systematics, morphology, cytotaxonomy, floristics, phytogeography, physiology, fire ecology, reproductive biology, dispersal and germination, and mycorrhizae. Habitats and plant communities discussed by contributors included, for example, wetlands, oak woodlands, chaparral, grasslands, the alpine, many desert types, and coniferous, mixed evergreen, and tropical deciduous forests. Geographic areas covered in papers included many regions of western North America (in Canada, U.S., Mexico) and portions of South America (e.g., Colombia and Ecuador). Plant groups investigated by our contributors are many, including myxomycetes, zygomycetes, bryophytes, hepatics, gymnosperms, and angiosperms. In addition, nine new taxa were described and four new combinations were made in volume 34.

My goals as Editor have been to guide authors through the review, revision, and

publication processes and to implement new journal policies that could enhance the editorial and managerial aspects of *Madroño*. To these ends, I can report a healthy journal with larger, more diverse issues than ever. Although this editor may not have been as prompt in responding to author's needs as some would have liked, and although a few authors were "extremely concerned" at times and found the process to be "very upsetting" or "increasingly objectionable", neither the reviewers nor the editors ever intended to be "venomous", "inattentive", "incoherent", "antagonistic", or "unreasonable". I recognize the "fallibility of editors and reviewers", as well as that of authors; but, hopefully, we strive for "careful and thorough editing" to correct errors of fact, lack of clarity, poor grammar, and inconsistent style. Our reviewers, in particular, have volunteered a considerable effort to provide generally "excellent editorial and technical comments", "valuable additions", and "helpful critiques", and they are an essential part of a peer-reviewed journal such as *Madroño*. The review and revision process is never meant to be "ludicrous", "counter productive", nor an "increasingly frustrating experience", but should be "a valuable learning experience" that often "improves the manuscript considerably". I trust we are all students of the plant sciences because of our love for the field and, within this, our desire for communication among our peers. The reviewers and editors, however, would be most appreciative of fewer hard knocks, and thus, friends, some of us could lighten-up a bit! A result of thorough preparation, patience, and good humor should be even better papers and, certainly, lower blood pressure. Best wishes to the new Editor! W. R. F. Jr. 30 Nov 1987.

REVIEWERS OF MANUSCRIPTS

The editors thank all reviewers for their assistance with manuscripts, and extend special thanks to those who reviewed several manuscripts published in 1987. We are grateful for your generous contributions of time and effort toward maintaining and improving the quality of papers published in *Madroño*. Reviewers for volume 34 are:

Spencer C. H. Barrett	Arthur Gibson	Arthur M. Phillips III
Jim A. Bartell	James R. Griffin	Donald J. Pinkava
Jerry M. Baskin	J. Robert Haller	David C. Randall
John H. Beaman	Lawrence R. Heckard	Philip W. Rundel
Meredith Blackworth	James Henrickson	John O. Sawyer Jr.
Robert Boyd	Richard Jensen	Robert A. Schlising
Jack H. Burk	Walter Knight	James Shevock
Ragan Callaway	Arthur R. Krucheberg	Bradley G. Smith
Judith M. Cann-Hilliker	Jochen Kummerow	James P. Smith Jr.
Mary Carroll	Harlan Lewis	Ted V. St. John
Annetta Carter	Jack Major	John L. Strother
Kenton L. Chambers	Charles T. Mason	Barry D. Tanowitz
Susan G. Conard	Robert J. Meinke	Barbara M. Thiers
Lincoln Constance	Louis V. Mingrove	Harry D. Thiers
William B. Critchfield	Richard A. Minnich	John H. Thomas
Christopher Davidson	Reid Moran	Robert F. Thorne
Frank W. Davis	James D. Morefield	B. L. Turner
Dorothy Douglas	Maynard M. Moseley	Thomas R. Van Devender
Barbara Ertter	Walter H. Muller	Frank Vasek
Marie Farr	Brad Musick	William A. Weber
William J. Ferlatte	Nalini M. Nadkarni	

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NEW PUBLICATION

REGALADO, JR., J. C., R. K. RABELER, and J. H. BEAMAN, *LABELS3 user's manual: Guide to development of a collection database*, Beal-Darlington Herbarium, Dept. Botany and Plant Pathology, Michigan State Univ., East Lansing, MI 48824-1312, 26 Jun 1987, [vi], 102 pp. (+ 5.25" computer disk), ISBN 0-9617739-0-1 (paperbound), price unknown. ["LABELS3 is a program package written in dBASE III Plus to produce herbarium specimen databases and make labels. With the associated programs QUERY and CHKLIST, the database can be queried for relevant information about a series of collections, and checklists can be made for the entire database or selected segments. A collection notebook can be generated from the database as an archival record of a set of collections. . . . LABELS3 is more than a label production program. Its primary objective is for developing and maintaining databases that can be queried for relevant information about collections and from which checklists can be produced."]—from preface. Requirements: IBM computer or compatible, 256 RAM, dBASE III Plus, WordStar.]

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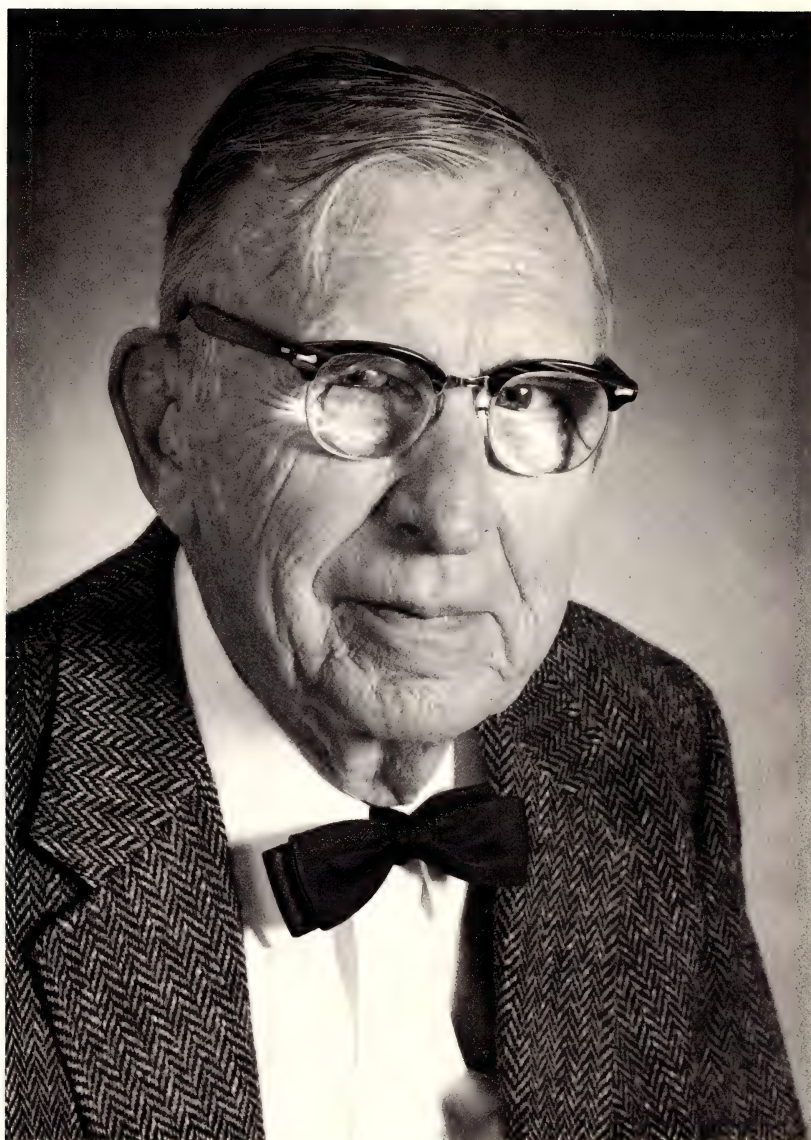
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Cornelius H. Muller, Professor of Botany, Emeritus, University of California, Santa Barbara, and Adjunct Professor of Botany, University of Texas, Austin, has stamped a broad impression on California botany. His personal influence has been a major force in determining the direction of research and thought in ecology, systematics, and evolutionary biology. Much of the research reported

in *Madroño* was directly influenced by Dr. Muller and his students or close associates.

Most people know Professor Muller as Ecologist or Systematist, but few are aware of his international stature in both fields. He has a record of accomplishment in a dozen or more subdisciplines, any one of which would be viewed by many of us as a successful lifetime achievement. Noteworthy examples include, but are not exhausted by, the following: pioneer plant explorer of Mexico; early advocate of the study of tropical botany; taxonomic authority in legumes, Solanaceae, and oaks; guayule specialist; chemical analyst of plant products; and botanical historian. He produced a definitive methodology for the study and evaluation of allelopathy and demonstrated the fundamental importance of allelopathy in California vegetation dynamics, he demonstrated the importance of ecological control in actual or potentially hybridizing populations, and he enunciated fundamental principles of the structure and evolution of vegetation.

That the pages of *Madroño* so thoroughly reflect Dr. Muller's influence shows the power of his teaching. Several of his classes and seminars are legendary at UCSB, but Dr. Muller taught all the time whether or not he always recognized it. The twenty years that I spent at his lunch desk provided my most broadening education! Hardly a lunch hour escaped without some new research subject being enunciated or some established ikon being devastated. The power of his insight and intellect on these occasions was inspiring but also humbling. A compliment from Dr. Muller was always genuine and stimulating.

The breadth and power of Dr. Muller's influence will continue to be felt for generations. Even now, there is a re-awakening of study of oaks that is multi-dimensional, but at the focal point of this activity remain Dr. Muller's established guidelines and new insights continued to flow from this fount of knowledge.

To Cornelius H. Muller this volume of *Madroño* is humbly and respectfully dedicated. — DALE M. SMITH, Professor of Botany, Emeritus, University of California at Santa Barbara, Red Maple Farm, HC-65, Box 100 BB, Windsor, KY 42565.

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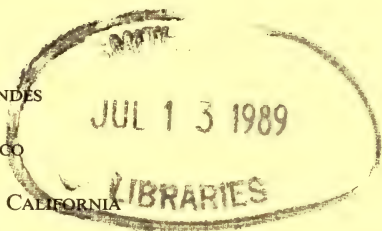
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MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

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THREE NEW SPECIES OF *GALIUM* FROM THE NORTHERN ANDES

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ABSTRACT

Three new species of *Galium* are named and described: *G. antuneziae* of Peru, with hairless fruits, shows some similarities to *G. mandonii* Britton, *G. cajamarcense* from Peru, also with hairless fruits, has a general resemblance to *G. corymbosum* R. & P. of sect. *Relbunium*, but lacks the involucre diagnostic of that section; *G. fosbergii* of Ecuador seems closest to *G. diffusoramosum* Dempster & Ehrendorfer, although the hairs are reduced in number and not uncinatate.

RESUMEN

Se nombran y describen tres nuevas especies de *Galium*: *G. antuneziae* de Perú, con frutos sin tricomas, muestra semejanzas con *G. mandonii* Britton, *G. cajamarcense* de Perú, también con frutos sin tricomas, se asemeja a *G. corymbosa* R. & P. de la sección *Relbunium*, pero carece del involucro diagnóstico de esa sección; *G. fosbergii* de Ecuador al parecer se relaciona con *G. diffusoramosum* Dempster & Ehrendorfer, aunque las tricomas de los frutos son escasos y no uncinulados.

In the course of my work on *Galium* sect. *Relbunium*, I have located three specimens that do not belong to that section nor to any named species of *Galium*. This paper is, therefore, a codicil to my three longer papers on South American *Galium* (Dempster 1980, 1981, 1982). I describe and name herein three new species based on these specimens.

Galium antuneziae Dempster, sp. nov. (Fig. 1).

Herba perennis semiprostrata, caulibus lignosis flexibilibus. Foliis in quoque verticillo quatuor, ellipticis, petiolo brevi. Floribus solitariis axillaribus pedunculo brevi; corollis rotatis, profunde divisis, albis, latitudine 2.5 mm; lobis ovatis apice gracili; ovariis fructibusque subtiliter tuberculatis.

Semi-erect perennials with long (to 50 cm) flexible woody stems ending in tufts of fine-textured herbage; young stems with narrow angles having short urceolate hairs. Leaves 4 at nodes, less than 8 mm long, elliptical, shortly petiolate with few short stoutish curved hairs, mostly on reflexed margins, ribs and pulvinate bases. Flowers perfect, solitary in axils, on short peduncles, scarcely exerted beyond leaves; corollas white, rotate, 2.5 mm across, deeply divided, the 4

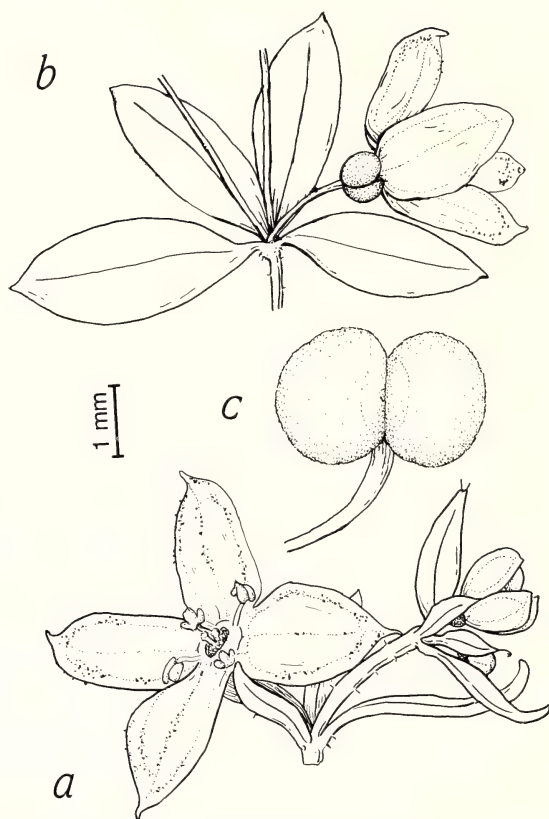


FIG. 1. *Galium antuneziae*. a. Flowering branchlet. b. Node with solitary flower. c. Young fruit. All illustrated from type, *Antunez de Mayolo 110*.

lobes ovate with short attenuated tips, glabrous externally, the interior surfaces with many glandular tack-shaped hairs scattered on the apical half; ovaries and fruits very finely tuberculate; fruits dry, 3 mm across; mericarps partially spherical, but flattened at juncture.

TYPE: Peru, Huancavelica, near Churcampá, 2500 m, on slopes bordering cultivated fields, *Antunez de Mayolo 110* (holotype: F; isotype: OBI).

PARATYPE: Near Churcampá at 3100 m, *Antunez de Mayolo 248* (UC), erroneously attributed to *G. mandonii* Britton (Dempster 1982).

Galium antuneziae shows some similarity to *G. mandonii* in that the leaves of both are narrowed to a petiole above a hairy pulvinate base, have narrow stem angles with numerous small retrorse hairs, and have short-pedicelled flowers solitary in axils. *Galium mandonii*, however, differs in having lax herbaceous stems above a fibrous root system, smaller corollas relative to ovaries, larger, narrower and more remote leaves, and 8-sulcate ovaries.

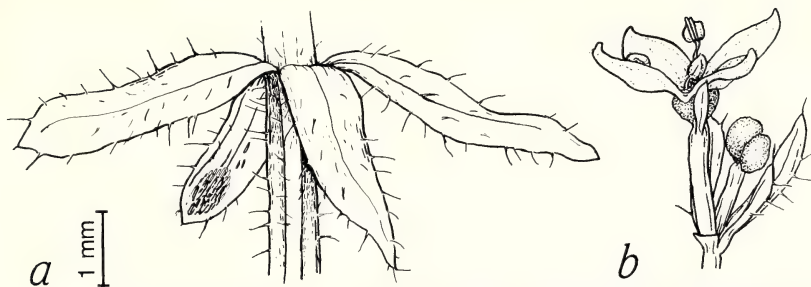


FIG. 2. *Galium cajamarcense*. a. Node. b. Flowering branchlet. Illustrated from type, Beck 7880.

The name is for the collector, whom I met in Peru in 1977, where she was studying indigenous dye plants, including *Galium*.

***Galium cajamarcense* Dempster, sp. nov. (Fig. 2).**

Herba perennis caespitosa caulibus foliisque pilis longis patentibus dispersis. Foliis in quoque verticillo quatuor, usque ad 4 mm, oblongis, internodia aequantibus. Floribus paucis, pedicellatis, ramulis brevibus foliosis insidentibus; corollis rotatis, profunde divisis, lobis ovatis obtusis; ovariis laevibus. Fructibus ignotis.

Tufted perennials to 6 cm tall, from creeping root system; stems and leaves with scattered long spreading hairs. Leaves 4 at nodes, ca. 4 mm long, about as long as internodes, oblong with abruptly acute unarmed apices; glandular cells in a dense subapical cluster. Flowers few, pedicellate, on short leafy axillary branchlets; corollas rotate, 2 mm across, deeply divided, the four lobes ovate, obtuse, glabrous; ovaries smooth. Fruits unknown.

TYPE: Peru, Dept. Cajamarca, 15 km southwest of Cajamarca at edge of Cumbe Mayo Park, 3400 m, "Cesped abierto pedregoso", Beck 7880 (holotype: UB).

This species bears a general resemblance to forms of *G. corymbosum* Ruiz & Pavon sensu lato of sect. *Relbunium*. Unlike that complex species, however, the flowers of *G. cajamarcense* are pedicellate and without involucre.

***Galium fosbergii* Dempster, sp. nov. (Fig. 3).**

Herba perennis scandens polygama, caulibus gracilibus lignosis; foliis in quoque verticillo quatuor, usque ad 6 mm, ovatis apicem tenuem versus angustatis, petiolatis, base tomentosis, margine costae et pagina superna pilis brevibus antrorsis instructis; floribus paucis ramulis insidentibus; pedicellis capillaribus usque ad 9 mm, exsertis; corollis rotatis, profunde divisis, lobis ovatis, obtusis; fructibus immaturis, pilis rectis sparse instructis.

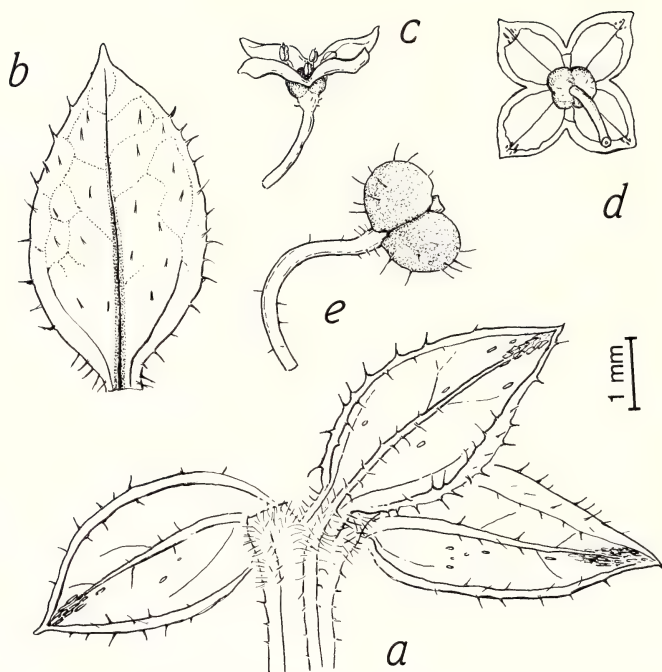


FIG. 3. *Galium fosbergii*. a. Node, showing under side of 3 leaves. b. Leaf, upper side, showing triple venation. c. Staminate flower. d. Same from below. e. Immature fruit. All illustrated from type, Fosberg and Giler 22945.

Lax, monoecious or polygamous perennials with slender woody stems, clambering or climbing to 35 cm; stems sparsely set with short retrorse hairs. Leaves 4 at nodes, up to 6 mm long, ovate, tapered to a slender apex and narrowed to a petiole above a hairy, often swollen and sometimes persistent base; leaves more or less obscurely 3-nerved, the upper surfaces set with short antrorse hairs, the lower surfaces glabrous except for the midribs. Flowers on few-flowered well exserted axillary branches; pedicels capillary, 1.5–9 mm long, well exserted beyond bracts; corollas rotate, 2 mm across, divided to near base, glabrous, the lobes ovate, obtuse. Fruits (immature) sparsely set with very short, straight, slightly antrorse spreading hairs.

TYPE: Ecuador, Loja, northeast slope of Cerro Mataperro, 1815 m, steep dry slope of decomposed slaty shale, tangled in bushes, Fosberg and Giler 22945 (holotype: US).

The often swollen and persistent leaf bases of *G. fosbergii* suggest a relationship with *G. diffusoramosum* Dempster & Ehrendorfer, of northern Chile. Characters of inflorescence, flowers, and leaves also are compatible with that species. The fruit hairs of *G. fosbergii*,

however, are not uncinata but, although sparse, they are straight as in sect. *Lophogalium*. Although fruit hairs are typically of taxonomic importance in *Galium*, I think that *G. fosbergii* represents a reduction in number and shape of hairs, rather than a closer relationship with sect. *Lophogalium*. The large geographical distance between *G. fosbergii* and *G. diffusoramosum* (ca. 2800 km) precludes the consideration of the former as an aberrant form of the latter.

ACKNOWLEDGMENTS

Thanks are owing to Alan Smith for criticising my Latin, and to Victoria Sosa for correcting my Spanish.

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(Received 10 Nov 1986; revision accepted 4 Oct 1987.)

NOTEWORTHY COLLECTION

ARIZONA

SALIX PLANIFOLIA Pursh. ssp. *PLANIFOLIA* (SALICACEAE). — Apache Co., Fort Apache Indian Reservation, White Mts., Smith Cieniga, along Ord Creek, 33°56'N, 109°35'W, 9890–10,000 ft, dominant in *Salix* thicket along creek, associated with *S. arizonica*, wet saturated soils of igneous origin, heavily browsed by elk, 9 Jul 1987, C.-E. Granfelt 87-1 (ARIZ, CAN). White Mts., Bull Cieniga, along Ord Creek, 33°55'30"N, 109°35'30"W, 10,240 ft, only *Salix* in saturated meadows and on slopes adjacent to creek, closely browsed by elk, 29 Jul 1987, C.-E. Granfelt 87-24, 87-25, 87-26 (CAN). Identified by George W. Argus.

Previous knowledge. Trans-subarctic-boreal from Alaska to Newfoundland south to New Hampshire and British Columbia extending southward in the cordillera to California and the mountains of northern New Mexico and Utah. Inclusion of Arizona in range given by Martin and Hutchins (Flora New Mexico, 1980) is undocumented.

Significance. New to the flora of Arizona. In Arizona this species seems to occur at somewhat lower elevations (10,000–10,240 ft) than it does in nc. New Mexico where it occurs at 10,500–11,500 ft. The species in the southern cordillera has usually been referred to var. *monica* (Bebb) C. Schneider. The status of this taxon is under study. — GEORGE W. ARGUS, National Herbarium, Museum of Natural Sciences, Ottawa, ON K1A 0M8, Canada and CARL-ERIC GRANFELT, Box 630, Pinetop, AZ 85935.

HILARIA ANNUA (GRAMINEAE), A NEW SPECIES FROM MEXICO

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ABSTRACT

Hilaria annua from the state of Colima, Mexico, is described as new. This, the first annual species known in the genus, is clearly related to *H. ciliata* (Scribn.) Nash. It differs from that species in its annual habit, somewhat smaller spikelets, and chromosome number which is tetraploid ($2n = 36$) rather than octoploid ($2n = 72$).

RESUMEN

Se describe **Hilaria annua** del estado de Colima, México como especie nueva. Se trata de la primera especie anual conocida para el género, la cual es similar a *H. ciliata* (Scribner) Nash. No solo se distingue por su condición anual, sino también por tener espiguillas algo más pequeñas y por el número cromosómico. La especie nueva es tetraploide ($2n = 36$) y *H. ciliata* es octoploide ($2n = 72$).

The genus *Hilaria* (s.l.) comprises a small group of grasses that inhabit arid and semi-arid regions and range from southwestern United States to Guatemala. The inflorescence is a narrow terminal spike, with spikelets borne in groups (fascicles) of three at the nodes, falling entire from the axis when mature. In each fascicle the two lateral spikelets are staminate and usually at least 2-flowered; the central one is 1-flowered, pistillate or perfect. Species of *Hilaria* fall quite naturally into two groups which currently are usually treated as subgenera. The distinctions characterizing these subgenera are summarized in the following key:

1. Glumes thin, membranous, not fused nor indurate at their bases; central spikelet 1-flowered, perfect Subgenus *Pleuraphis*
1. Glumes indurate, fused at their bases; central spikelet pistillate Subgenus *Hilaria*

In the most recent revision of the genus *Hilaria* (Sohns 1956), nine species and one variety are recognized. Sohn's stated that taxa in both subgenera are remarkably uniform vegetatively: i.e., all are strong perennials and most are either stoloniferous or rhizomatous. It was somewhat of a surprise, therefore, when we encountered what appeared to be a weedy annual *Hilaria* growing in abundance in two different areas a short distance south of Cd. Colima, México. These plants are members of the subgenus *Hilaria* and superficially resemble *H. ciliata* (Scribn.) Nash, a species also found in that region.

They differ not only in being annual, but in having smaller spikelets and a chromosome number of $2n = 36$. All chromosome counts of *H. ciliata* reported to date are $2n = 72$.

Our gatherings were made in 1974. Since that time we have seen no other collections of an annual *Hilaria*, nor does McVaugh (1983) mention any annual species in his treatment of this genus. Differences which separate plants of our collections from others in the group, however, suggest that they represent a previously unrecognized species which is described below.

***Hilaria annua* J. & C. Reeder, sp. nov. (Fig. 1).**

Gramina annua, caespitosa; culmi 40–50(–60) cm alti, erecti vel interdum geniculato-adscendentes, nodis radicanes, papilloso-pilosis; culmi gracili, glabri, ramosi. Vaginae glabrae vel plus minusve papilloso-pilosae, quam internodiis breviores; ligula membranaceo-hyalina, ciliata, 2–3 mm longa; laminae 10–20(–30) cm longae, usque ad 3.5–5 mm latae, planae, plerumque glabrae sed supra interdum sparsim papilloso-pilosae, marginibus scabrae. Spicae usque ad 5 cm longae, densiflorae, articuli rhachis 4–4.5 mm longi, plani, gracillimi, ca. 0.3 mm lati, marginibus brevi ciliati; fasciculi 4–4.5 mm longi, pallidi vel niger-purpurascens. Glumae induratae, papillo-sae, plus minusve valde nervosae, marginibus scabri vel brevi ciliati; spiculae laterales masculae, plerumque uniflores, interdum bi- vel triflores, lemmata hyalina, ca. 3.5 mm longa, 3-nervis. Antheris ca. 2 mm longis; spicula intermedia uniflora, feminina, lemmata ampulliforma, 3-nervis, ca. 4.5 mm longa, basi hyalini, apice aliquanti apicibus membranacibus. Caryopside translucida, ca. 1.8–2 mm longa, embryo fuscus, caryopsidi fere aequilongus. Chromosomatum numerus: $2n = 36$.

Plants annual, caespitose; culms 40–50(–60) cm tall, slender, glabrous, branching, erect to somewhat ascending and rooting at the papillose-pilose nodes. Sheaths shorter than the internodes, glabrous or more or less papillose-pilose; ligule membranous-hyaline, ciliate, 2–3 mm long; blades flat, 10–20(–30) cm long, 3.5–5 mm wide, mostly glabrous but sometimes sparsely papillose-pilose on the adaxial surface, the margins scabrous. Spikes (3.5–)4–5 cm long, densely flowered, the rachis joints flat, slender, 2.5–4 mm long and ca. 0.3 mm wide, the margins ciliolate; fascicles 3.5–4.5 mm long, pale or becoming somewhat blackish-purple. Glumes indurate, minutely papillose, the nerves prominent, especially toward the apex, the margins scabrous to ciliolate; lateral spikelets staminate, mostly 1-flowered, sometimes 2- or 3-flowered, lemma hyaline, 3-nerved, about as long as the glumes. Anthers ca. 2 mm long; central spikelet pistillate, 1-flowered, the glumes slightly shorter than the fascicle, with one (rarely two) lateral, flattened, scabrous to short-ciliate awns,



FIG. 1. *Hilaria annua*. Photograph of the holotype (J. R. & C. G. Reeder 6333).

these reaching to the apex of the glume; lemma flask-shaped, ca. 4.5 mm long, 3-nerved, basal portion hyaline, the upper part somewhat membranous. Caryopsis whitish, translucent, 1.8–2 mm long, the embryo brownish, nearly as long as the grain. Chromosome number: $2n = 36$.

TYPE: MEXICO: Colima, 10 km s. of Cd. Colima, abundant along roadside with other rank weeds, 300 m, 24 Sep 1974, *J. R. & C. G. Reeder 6333* (holotype: ARIZ; isotypes: MEXU, MICH, RM, US).

PARATYPE: MEXICO: Colima, 5 km s. of Cd. Colima, frequent with other weeds amongst thorny shrubs, 430 m, 24 Sep 1974, *J. R. & C. G. Reeder 6331* (ARIZ, RM, UC, US). This collection certainly represents the same species, but exhibits minor differences. The plants are clearly annual, but more profusely branched, and the culms tend to be more ascending, some of them rooting at the lower nodes. The shorter spikes average 2–3 cm long rather than 4–5, and the fascicles are slightly smaller, averaging 3.5–4 mm long, rather than 4.0–4.5 mm as in the type. The chromosome number of this collection also was determined as $2n = 36$.

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(Received 30 Mar 1987; revision accepted 30 Sep 1987.)

ANNOUNCEMENT

NEW PUBLICATION

GRIFFIN, J. R., P. M. McDONALD, and P. C. MUICK, compilers. 1987. *California oaks: a bibliography*. U.S.D.A. Forest Service, Pacific Southwest Forest and Range Experiment Station, Gen. Tech. Rep. PSW-96, Berkeley, CA. 38 pp. [California oaks continue to attract considerable attention among natural resource professionals. This report provides a comprehensive bibliography of the extensive but scattered oak literature. The 768 references are organized into two systems: (a) a topical outline, in which references are displayed under key word headings and subheadings, and author-date entries that help to locate items by researcher or date; and (b) a *Quercus* species index, in which references contain serial numbers for all species and hybrids. Single copies are available from Pacific Southwest Forest and Range Experiment Station, 1960 Addison Street, Berkeley, CA 94704.]

A NEW *ENCELIA* (ASTERACEAE: HELIANTHEAE)
FROM BAJA CALIFORNIA

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ABSTRACT

Encelia densifolia Clark & Kyhos, from the isolated Picachos de Santa Clara in northern Baja California Sur, is morphologically distinctive, having short peduncles, broad obovate phyllaries, and remotely dentate leaves.

RESUMEN

Encelia densifolia Clark & Kyhos, de los aislados Picachos de Santa Clara en el norte de Baja California Sur, es distinto morfológicamente, con pedúnculos cortos, filarios largos y obovados, y hojas remotamente dentadas.

In 1947, H. S. Gentry made two collections of a new *Encelia* from the Picachos de Santa Clara that he later labeled "*Encelia densifolia*", but never formally published. We have recollected the species and studied it in the field and in cultivation to understand better its relationships with other members of the genus, and describe it here.

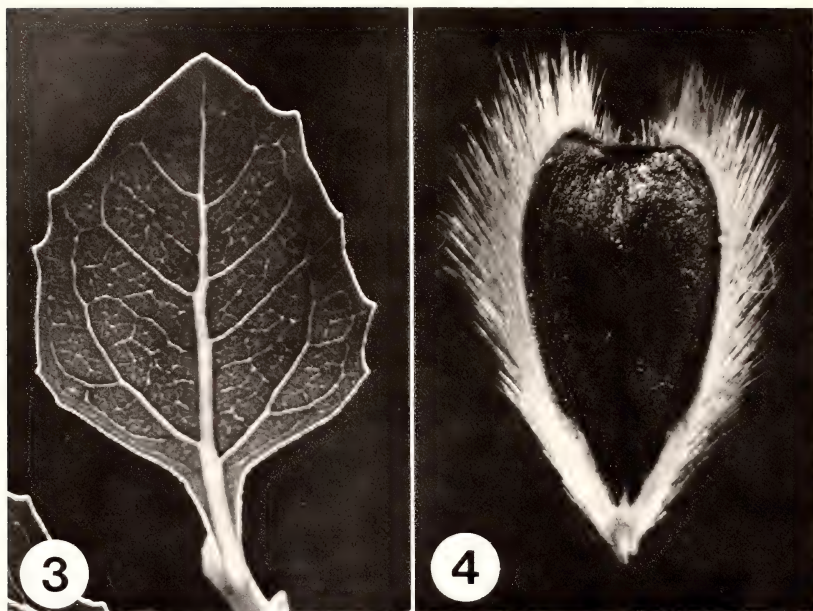
***Encelia densifolia* Clark & Kyhos, sp. nov.**

Encelia densifolia H. S. Gentry, nom. ined. herb., *Gentry 7757*, 5–10 Nov 1947.

Frutex erectus vel aliquantum effusus, usque ad 1.5 m altus. Folia 14–65 mm longa, 7–35 mm lata, griseo-prasina, pilosa, rigide divergentia vel ascendentia, ovata, plerumque dentata, petiolis alatis. Capitula solitaria, floribus 20–30 mm latis trans flores radiantes, fructibus plerumque pendula. Pedunculi breves (7–30 mm longi), minute pubentes. Involucra 11–15 mm longa, 9–13 mm lata. Phyllaria 3–6 mm lata, 7–10 mm longa, imbricata, obovata, minute pubentia, marginibus ciliatae. Flores radiantes 7–12 mm longi, flavi, lucem ultravioleaceum reflectentes. Flores disci flavi, lucem ultravioleaceum absorbentes. Antherae porphyreae aureae. Stigmata flava. Achenia obovata, compressa, in superficie plana glabra pro parte



FIGS. 1, 2. *Encelia densifolia* (Clark 585). 1. Capitulum in flower. 2. Capitulum in early fruit, showing pendulous habit and enlarged phyllaries. Photographs taken in the field in the vicinity of the type specimen ($\times 2.2$).



FIGS. 3, 4. *Encelia densifolia*. 3. Leaf (transilluminated to emphasize venation), $\times 2$. 4. Achene, $\times 10$. Photographs taken of plants grown from seed (Clark 585) in outdoor cultivation.

maxima, in margine ciliata, sine aristis, ad apicem incisura lata et non profunda. Chromosomatum gametophytorum numerus 18 (Figs. 1–4).

Erect or occasionally spreading shrub, to 1.5 m tall. Leaves 14–65 mm long, 7–35 mm wide, gray-green, pilose, rigidly divergent or ascending, ovate, usually remotely dentate, petioles winged. Capitula solitary, 20–30 mm wide across the rays in flower, pendulous in fruit. Peduncles short (7–30 mm long), minutely pubescent. Involucre 11–15 mm long, 9–13 mm wide. Phyllaries 3–6 mm wide, 7–10 mm long, imbricate, obovate, minutely pubescent, margins ciliate. Ray florets 7–12 mm long, yellow, reflecting ultraviolet. Disc florets yellow, absorbing ultraviolet. Anthers brown or yellow. Stigmas yellow. Achenes obovate, flattened, mostly glabrous on the face, ciliate on the margin, without awns, with a broad shallow apical cleft. Chromosome number $n = 18$.

TYPE: Mexico, Baja California Sur: Picachos de Santa Clara, 13.6 mi nw. of San Ignacio-Abrejos road at a point 24.7 mi ne. of Punta Abrejos, 300 m, 24 Mar 1981, C. Clark 585 (holotype: CAS; isotypes: DAV, CSPU, RSA, UC; all material is from the same plant).

PARATYPES: Mexico, Baja California Sur: n. slope and in arroyo,

Picachos de Santa Clara, 28 Dec 1975, *Moran* 22758 (DAV, SD). Las Tinajas and vicinity in cerros e. of Los Picachos de Santa Clara, 21–23 Mar 1947, *H. S. Gentry* 7560 (SD). Picachos de Santa Clara, Arroyo de los Picachos, 5–10 Nov 1947, *H. S. Gentry* 7757 (SD).

Distribution and habitat. Existing collections of the species may correspond to only two populations. *Clark* 585 and *Moran* 22758 are from the same location. We suspect *Gentry* 7757 is also from this location; Arroyo de los Picachos may be Arroyo Tecolote, which is the major southeast drainage of the range (*Moran* pers. comm.) and the location of the other two collections. *Gentry* 7560 represents the other known population. It is possible that there are other undiscovered populations in this rugged mountain range, but the species does seem to be endemic to it.

The holotype grew along a dry stream-course. Over 100 plants were found up to 30 m higher on the gravelly slopes above it, primarily on the north-facing shoulder of the southeastern-most peak. Surrounding vegetation was desert scrub, and *E. densifolia* was co-dominant with species of *Bursera*, *Ferocactus*, and *Lycium*.

Morphology. *Encelia densifolia* can easily be distinguished from other species in the genus. The peduncles are short enough that the heads are partially submerged in the leaves, a feature otherwise found only in *E. ventorum*, which has finely divided leaves (*Kyhos et al.* 1981). The remote dentation of the leaf margin and the obovate phyllaries are unique in the genus.

The phyllaries are the broadest in the genus. *Werk and Ehleringer* (1983) found that photosynthesis by phyllaries and paleae in *E. farinosa* and *E. californica* did not contribute much to the overall energy budget of the plant. We suspect the form of the *E. densifolia* phyllaries, in conjunction with the generally nodding fruiting heads, may be an adaptation for increased photosynthesis by exposing these organs to direct sunlight.

The leaf and phyllary pubescence consists of multicellular uniseriate hairs of the sort that are ubiquitous in the Heliantheae. The junctions between cells are slightly swollen (Fig. 5). Although the trichomes form a continuous covering over the surface, the leaves are not as reflective as those of other species such as *E. palmeri* and *E. farinosa* (*Harrington and Clark* unpubl.). The trichomes also are easily wettable, and are less reflective when wet. On foggy summer days, common in the region, the wet leaves would absorb more light for photosynthesis without adversely increasing water loss or leaf temperature.

Relationships. The ultraviolet-reflecting rays (*Clark and Sanders* 1986) and the possession of a suite of benzopyran and benzofuran secondary metabolites (*Proksch and Clark* 1987) are apomorphies

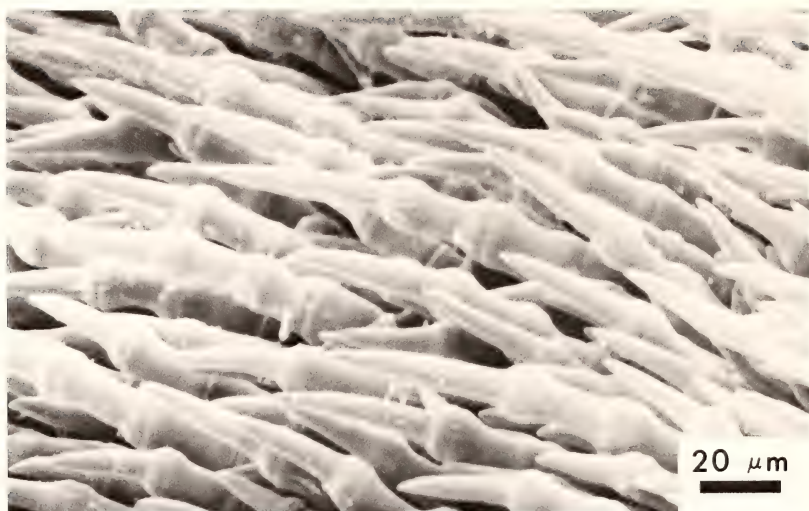


FIG. 5. Scanning electron micrograph of the trichomes of the adaxial leaf surface of *Encelia densifolia* (Clark 585).

linking *E. densifolia* to the clade containing the other Baja California species *E. farinosa*, *E. californica*, *E. palmeri*, *E. ventorum*, *E. conspersa*, and *E. asperifolia*. Its yellow discs are not found in other *Encelia* species of the region, and, along with other features, suggest that *E. densifolia* is basal in this clade (although its autapomorphies argue against any consideration of it as “primitive”).

Hybridization. In cultivation, *E. densifolia* forms fertile hybrids with every other *Encelia* species to which it is crossed; all other *Encelia* species are equally interfertile (Kyhos et al. 1981). In the natural environment, it is sympatric with *E. farinosa* and occurs near *E. palmeri*. Although we saw no hybrids in the field, two collections [Gentry 7559 (SD, UC), and 7587 (UC)] labeled “*Encelia viscaínoensis*” appear intermediate between *E. densifolia* and one of these species. Progeny testing of several dozen achenes collected from an *E. densifolia* plant growing among *E. farinosa* yielded no hybrid plants, but we crossed the species in cultivation and obtained hybrids resembling “*viscaínoensis*” in leaf morphology, so it is likely that the “*viscaínoensis*” collections represent field hybrids between these species.

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ANNOUNCEMENT

OREGON ENDANGERED SPECIES PROGRAM

In September, 1987, Oregon Senate Bill 533, popularly known as the Oregon Endangered Species Act, was passed into law. One of the provisions of this legislation is the establishment of a threatened and endangered species program under the direction of the state Department of Agriculture. This new program was activated in February of this year, with early goals being the development of rule-making procedures for state listing of threatened and endangered plants, the initiation of a review process to facilitate the ranking of candidate species, and the establishment of research projects focusing on biological aspects of rarity in the flora of the Pacific Northwest.

The Oregon Department of Agriculture is anxious to interact with individuals and organizations with an interest in the sensitive plant species of Oregon and adjacent states. Inquiries pertaining to the review process, listing procedures, research, or questions concerning particular taxa, should be addressed to: R. Meinke, Coordinator, Endangered Species Program, Plant Division, ODA, 635 Capitol Street NE, Salem, Oregon 97310-0110.

NOTA SOBRE EL GENERO *COMMELINA* (COMMELINACEAE) EN EL VALLE DE MÉXICO CON CAMBIOS EN LA NOMENCLATURA DE ALGUNAS DE SUS ESPECIES

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RESUMEN

Como resultado de la revisión del género *Commelina*, efectuada para el volumen III de la Flora Fanerogámica del Valle de México, se reconoce la existencia de 7 especies, de las cuales 4 (*C. coelestis* Willd., *C. dianthifolia* DC., *C. diffusa* Burm. f. y *C. erecta* L.) se aceptan en la circunscripción y nomenclatura usualmente empleadas. En cuanto a las 3 restantes: el nombre *C. orchioides* Booth ex Lindl. substituye por prioridad a *C. alpestris* Standl. & Steyerl.; el de *C. pallida* Willd. es necesario restituir para las plantas de la región generalmente identificadas como *C. texcocana* Matuda y *Phaeosphaerion leiocarpum* (Benth.) Hassk.; el de *C. tuberosa* L., en cambio, se aplica a las determinadas como *C. coelestis* var. *bourgeaui* Clarke.

ABSTRACT

In the treatment of the genus *Commelina* for the "Flora Fanerogámica del Valle de México" seven species are recognized, four of which (*C. coelestis* Willd., *C. dianthifolia* DC., *C. diffusa* Burm. f. and *C. erecta* L.) are accepted in their usual circumscription and nomenclature. As to the remaining three: the name *C. orchioides* Booth ex Lindl., for reasons of priority, replaces *C. alpestris* Standl. & Steyerl.; the name *C. pallida* Willd. is rescued for local plants usually identified as *C. texcocana* Matuda and *Phaeosphaerion leiocarpum* (Benth.) Hassk.; and the name *C. tuberosa* L. applies to those determined as *C. coelestis* var. *bourgeaui* Clarke.

Antes de que llegara el turno de revisar las Commelinaceae para el volumen III de la Flora Fanerogámica del Valle de México, se podía prever que ésta no iba a ser una familia sencilla de estudiar.

A través del tiempo y según el criterio de diferentes autores, diversos miembros de las Comelináceas han estado cambiando de nombres y de situación taxonómica, no sólo a nivel de especie sino también de género. Para el Valle de México resultó ser *Commelina* que, conteniendo mayor número de especies, presentó asimismo más problemas.

En general, las plantas correspondientes a *Commelina* son muy atractivas, tanto por su follaje como especialmente por sus flores vistosas, razón por la cual se hallan prodigamente representadas en los herbarios; en total se examinaron más de 500 especímenes. Además se consultaron microfichas del herbario de Humboldt y Bonpland, del herbario Linneano y del herbario de Willdenow.

A pesar del considerable número de ejemplares conservados en

las instituciones, a menudo se nota inseguridad en las identificaciones y una gran proporción del material revisado cambió de nombre al aplicar las conclusiones a las que se llegó al finalizar este trabajo.

Uno de los problemas serios para el estudio de individuos herborizados de *Commelina* lo constituye la dificultad para observar las características de las flores, ya que éstas son frágiles y delicadas y presentan el fenómeno de delicuescencia, conservándose mal en los ejemplares de herbario. Es por ello que ha resultado indispensable hacer observaciones de cada una de las especies también en el campo.

De manera opuesta a lo que sucede en los herbarios, la bibliografía sobre este grupo es relativamente escasa y se encuentra bastante dispersa.

Hemsley (1885) y Reiche (1914), de acuerdo con Clarke (1881), citan del Valle de México las siguientes especies y variedades: *Commelina coelestis* Willd., *C. dianthifolia* DC., *C. graminifolia* HBK., *C. graminifolia* var. *stricta* (Desf.) Clarke, *C. pallida* Willd., *C. quitensis* var. *cardiosepala* (Kunze) Clarke (var. "*cardiophylla*", según Reiche) y *C. tuberosa* L.; Reiche agrega asimismo *C. scabra* Benth.

La puesta al día más reciente para las Comelináceas mexicanas la constituyen los trabajos de Matuda (1956a, b), en los cuales se intenta depurar algunos de los criterios de Clarke y donde se mencionan para nuestra región: *C. alpestris* Standl. & Steyerf., *C. coelestis* Willd. (con *C. pallida* Willd. como sinónimo), *C. coelestis* var. *bourgeauii* Clarke, *C. dianthifolia* DC., *C. diffusa* Burm. f., *C. scabra* Benth. y *C. texcocana* Matuda, además de *Phaeosphaerion leiocarpum* (Benth.) Hassk. Sánchez (1969) sigue esta misma disposición.

El grupo evidentemente requiere de una revisión crítica a nivel continental y el presente estudio no puede resolver todos los problemas inherentes. Los resultados obtenidos, en ocasiones aún tentativos, llevan a reconocer 7 especies para el Valle de México: *C. coelestis* Willd., *C. dianthifolia* DC., *C. diffusa* Burm. f., *C. erecta* L., *C. orchiodes* Booth, *C. pallida* Willd. y *C. tuberosa* L.

1. *COMMELINA COELESTIS* Willd., Enum. Hort. Berol. 1:69. 1909.

Es una especie vistosa, más bien alta y tosca, erecta, de hojas largas y anchas, con la base envainadora; flores de 2 a 3 cm de ancho, de color azul intenso. Común en matorrales, pastizales o bosques de encino y pino, en altitudes entre 2250 y 2750 m.

Coincidimos con la acepción general de este nombre en la literatura y los herbarios; diferimos en considerar como sinónimo a *C. pallida* Willd., que es especie distinta. Un gran número de ejemplares del Valle de México concuerda bien con la imagen del tipo, depositado en el herbario de Willdenow. Existen, sin embargo, individuos con características intermedias entre *C. coelestis* y *C. orchiodes* y también entre *C. coelestis* y *C. tuberosa*. A este respecto véase también la discusión sobre la última especie.

2. *COMMELINA DIANTHIFOLIA* DC. in Redouté, Lil. 7. Tab. 390. 1812.

Erecta o suberecta, delicada tanto en sus tallos delgados y hojas angostas, como en sus espatas florales largamente acuminadas; flores de aproximadamente 2 cm de ancho, de color azul intenso. Habita en matorrales, pastizales, encinares y bosques de *Abies*; ampliamente distribuida en altitudes entre 2250 y 3000 m.

Bastante bien definida en bibliografía y herbarios, aunque no faltan individuos intermedios entre esta especie y *C. tuberosa*.

3. *COMMELINA DIFFUSA* Burm. f., Fl. Ind. 18, pl. 7, f. 2. 1768.

C. nudiflora sensu Burm. f., Fl. Ind. 17, non L.

C. longicaulis Jacq., Coll. Bot. 3:334. 1789.

Rastrera a ascendente, ramificada, tallos delgados, radicales en los nudos inferiores; flores de unos 2 cm de ancho, de color azul intenso. Colectada principalmente en matorrales y pastizales; ampliamente distribuida entre 2300 y 2750 m.

Hemsley y Reiche no la citan, debido probablemente a que Clarke, aun cuando hace mención de "*C. nudiflora* L.", no la refiere específicamente para México. Por lo general bien determinada en los herbarios, donde con frecuencia se le encuentra nominada con alguno de los sinónimos.

4. *COMMELINA ERECTA* L., Sp. Pl. 41. 1753.

Más bien erguida, se distingue de las demás por tener las espatas connadas en su extremo posterior y las flores con 2 pétalos de color azul claro, de alrededor de 1 cm de largo y el tercero unas 10 veces más pequeño que los anteriores, de color amarillo con blanco. Planta de afinidades termófilas, escasísima (¿ausente en la actualidad?) en el Valle de México.

No se ha encontrado citada con anterioridad para esta región, con excepción de Matuda, quien, en sus "*Commelináceas mexicanas*" (1956a), señala la existencia de *C. erecta* var. *angustifolia* (Michx.) Fern., en base a la colecta de Purpus 14327 de "San Carlos, D.F.", de septiembre de 1930; ésta no se menciona en las "*Commelináceas del Estado de México*" (Matuda 1956b). Posiblemente se trata de un error, pues la localidad no resulta familiar y casi no se conocen colectas de Purpus del Distrito Federal.

Sin embargo, en los herbarios ENCB y MEXU se encuentran ejemplares de Lyonnet 588, colectados en el Pedregal de San Angel en agosto de 1930, pertenecientes a *C. erecta*. Además se han visto los siguientes especímenes: 1. "C. de Azompan, Tequezquahuac, Agosto 1º, 1954, en matorral alto bosque secundario a 2860 m de

altitud", *Matuda 31196* (MEXU). Tal altitud resulta excesiva para esta especie y la localidad dudosamente pertenece al Valle de México. 2. "Valle de México, Distrito Federal, VI 1946", *M. Sánchez R. s.n.* (ENCB). 3. "Al oeste de Los Remedios, cerca de Naucalpan, cerca del río, 15 VIII 1966", *M. Rodríguez s.n.* (ENCB). Estas dos últimas colectas fueron hechas por alumnos y no es imposible que las localidades estén equivocadas.

5. *COMMELINA ORCHIOIDES* Booth ex Lindl., Bot. Reg. Misc. 53. 1838.

C. variabilis Schlecht., Ind. Sem. Hort. Hal. 7:13. 1838.

C. scapigera Kunth, Enum. Pl. 4:46. 1843.

C. alpestris Standl. & Steyerl., Publ. Field Mus. Nat. Hist., Bot. Ser. 23:213. 1947.

Planta más bien baja, escaposa o subescaposa; flores de 2 a 3 cm de ancho, de color azul intenso. Presente en pastizales y bosques de encino o de coníferas de regiones montañosas, en altitudes entre 2800 y 3500 m.

Commelina alpestris es el nombre más difundido en los herbarios, pero como lo apuntó Rohweder (1956), tal binomio no es el más antiguo para esta especie, por cierto bastante variable y común en el centro de México. *C. orchioides* tiene prioridad de varios meses sobre *C. variabilis*, ambas descritas a base de materiales cultivados procedentes de Real del Monte, Hidalgo. *C. scapigera*, aunque mencionada desde 1832, al parecer no fue formalmente publicada sino hasta 1843. Clarke (1881), desde hace tiempo reconoció que los últimos tres binomios corresponden a un solo taxon, pero a su vez los consideró como sinónimos de *C. elliptica* HBK., descrita a base de ejemplares de la costa de Venezuela. Aparentemente ni en el herbario de París ni en el de Berlín existen materiales originales de *C. elliptica*, pero su protólogo señala tantas diferencias con respecto a la especie mexicana de alta montaña, que el nombre en cuestión debe rechazarse para nuestra planta.

6. *COMMELINA PALLIDA* Willd., Hort. Berol. 2:87. 1816.

C. texcocana Matuda, An. Inst. Biol. Méx. 24:60. 1955.

Planta hasta de 2.5 m de alto, por lo común muy ramificada y sarmentosa; flores de alrededor de 1.5 cm de ancho, de color-violáceo claro. Habita en matorrales y a veces en bosque perturbado de encino, principalmente del oeste y sur del Valle, en altitudes entre 2300 y 2600 m.

El tipo de *C. texcocana* coincide bastante bien con la fotografía del material original de *C. pallida* y es idéntico a plantas reciente-

mente colectadas entre San Juan del Río y Querétaro, de donde proviene también tal material. En los herbarios revisados, la mayor parte de los ejemplares de *C. pallida* se encontraban identificados como *C. texcocana* Matuda o equivocadamente como *Phaeosphaerion leiocarpum* (Benth.) Hassk., especie de clima caliente y frutos carnosos.

En apariencia corresponde aquí igualmente lo referido por Clarke (1881) y Hemsley (1885) como *C. quitensis* var. *cardiosepala* (Kunze) Clarke y por Reiche (1914) como *C. quitensis* var. *cardiophylla* (sic), ya que la descripción original de *C. cardiosepala* Kunze concuerda de manera aceptable con *C. pallida*.

7. COMMELINA TUBEROSA L., Sp. Pl. 61. 1753.

C. graminifolia HBK., Nov. Gen. Sp. Pl. 1:258. 1815.

C. graminifolia var. *stricta* (Desf.) Clarke in A. DC., Monogr. Phaner. 3:152. 1881.

C. coelestis var. *bourgeaui* Clarke in A. DC., Monogr. Phaner. 3:153. 1881.

Más bien delicada, de tallo único o poco ramificado, delgado, hojas angostas, espatas cortas, abruptamente agudas, flores de 2 a 3 cm de ancho, de color azul intenso. Común, ampliamente distribuida en matorrales, pastizales, bosques de encino o de coníferas, en altitudes entre 2300 y 3100 m.

La mayor parte de los ejemplares de herbario se encontraron identificados como *C. coelestis* var. *bourgeaui*; sin embargo, al comparar las fotografías de tipos de esta última y de *C. tuberosa* L., no se hallaron mayores diferencias y más que todo, el estudio de las poblaciones en el campo indicó que, al parecer, no existe en México más que una sola entidad biológica que corresponde a los tipos en cuestión.

A la misma conclusión ha llegado Rohweder (1956), quien ubicó además a *C. coelestis* en la sinonimia de *C. tuberosa*.

Las observaciones en el Valle de México llevan a la conclusión que *C. tuberosa*, *C. coelestis*, *C. dianthifolia* y *C. orchioides* están muy emparentadas entre sí y al parecer pueden cruzarse con frecuencia. Sólo un estudio más profundo y más extenso podrá determinar si conviene mantenerlas como especies separadas o más bien considerarlas como variedades de *C. tuberosa*.

Algunos especímenes han sido erróneamente determinados como *C. scabra* Benth. y de ahí tal vez derivan las citas de esta última para el Valle de México (Reiche 1914, Matuda 1956b). Se trata, al parecer, de una especie independiente, caracterizada por flores de color rojizo, de cuya presencia en la región no se tiene certidumbre.

A continuación se proporciona una clave para separar las siete especies involucradas.

1. Espata connada en su extremo posterior, el cual es recto o casi recto; pétalo inferior mucho más pequeño (1.5 mm de largo por menos de 1 mm de ancho) que los dos pétalos superiores; planta escasa (probablemente ya inexistente) en el Valle de México, sólo conocida con seguridad del Pedregal de San Angel 4. *C. erecta*
1. Espata libre en su extremo posterior, el cual por lo general es redondeado; pétalo inferior semejante en forma y tamaño a los dos superiores.
 2. Raíces cilíndricas, no tuberosas; plantas por lo general rastre-
ras a ascendentes o sarmentosas, rara vez erectas, profusa-
mente ramificadas al menos en la madurez, las ramificaciones
divergentes; pétalos por lo general de menos de 1 cm de largo
y 1 cm de ancho.
 3. Planta rastrera a ascendente, rara vez erecta, más bien
delicada, con tallos por lo general de menos de 5 mm de
diámetro (en la parte basal, en vivo); pétalos de color azul
intenso, el inferior cortamente unguiculado, con una uña
de ± 1 mm de largo por ± 1 mm de ancho 3. *C. diffusa*
 3. Planta a menudo sarmentosa, con tallos robustos, por lo
general de más de 5 mm de diámetro (en la parte basal,
en vivo); pétalos de color azul-violáceo claro, el inferior
subsésil, con una uña de ± 0.5 mm de largo por ± 0.5 mm
de ancho 6. *C. pallida*
 2. Raíces tuberosas, fusiformes; plantas erectas, de tallo único o
poco ramificado, con las ramificaciones ascendentes; pétalos
por lo general de más de 1 cm de largo y 1 cm de ancho.
 4. Plantas escaposas o subescaposas, por lo general de menos
de 30 cm de alto, con hojas principalmente basales; pe-
dúnculo (uno o varios desde la base) largo, muy recto, con
una sola espata terminal; habita en altitudes de 2800 m o
más 5. *C. orchioides*
 4. Plantas con tallos bien definidos, simples o algo ramifi-
cados, por lo general de más de 30 cm de alto, con varias
a numerosas espatas terminales o axilares; plantas de al-
titudes por lo general inferiores a 2800 m.
 5. Hojas ampliamente lanceoladas, de más de 2.5 cm de
ancho, con la base amplexicaule 1. *C. coelestis*
 5. Hojas estrechamente lanceoladas a lineares, de 2.5 cm
o menos de ancho.
 6. Espata floral corta, abruptamente aguda; hojas por
lo general lanceoladas, de 0.6 a 1 cm de ancho ...
..... 7. *C. tuberosa*
 6. Espata floral largamente acuminado-caudada; hojas
por lo general lineares, de 0.2 a 0.7 cm de ancho .
..... 2. *C. dianthifolia*

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ANNOUNCEMENT

NEW PUBLICATIONS

NOBLE, W. J., AHTI, G. F., OTTO, and I. M. BRODO. 1987. *A second checklist and bibliography of the lichens and allied fungi of British Columbia*. Syllogeus 61. ISSN 0704-576X. [Syllogeus is a publication of the National Museum of Natural Sciences designed to permit rapid dissemination of information pertaining to the disciplines and educational functions for which the Museum is responsible. Articles are published in English, French, or in both languages, and issues appear at irregular intervals. Individual copies of no. 61 and a list of other publications from the Syllogeus series are available by mail from the National Museum of Natural Sciences, Ottawa, Ontario, Canada K1A 0M8.]

RUSHFORTH, K. D. 1987. *Conifers*. Facts on File Publications, New York. ISBN 0-8160-1735-2, \$24.95. [Topics covered include, biology of conifers, conifers in the garden, dwarf conifers, propagation, planting and replanting, pests and diseases, and a gazetteer of conifers. The gazetteer comprises over half of the book.]

A NEW SECTION OF *CLITORIA* SUBGENUS *NEUROCARPUM* (LEGUMINOSAE)

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ABSTRACT

Clitoria subgenus *Neurocarpum* sect. **Mexicana**, sect. nov. is described including ser. nov. **Mexicana**, **Tucumania**, and **Americana**. Section *Mexicana* is contrasted with sect. *Tanystyloba* and sect. *Neurocarpum*. Series *Mexicana* includes *C. humilus* Rose, *C. mexicana* Link, *C. monticola* Brandegees, *C. polystachya* Benth., and *C. triflora* Wats. Series *Tucumania* includes *C. cordobensis* Burk. Series *Americana* includes *C. fragrans* Small and *C. mariana* L. A key to species of sect. *Mexicana* is provided.

RESUMEN

Se describe *Clitoria* subgénero *Neurocarpum* sección **Mexicana**, secc. nov., e incluye las ser. nov. **Mexicana**, **Tucumania** y **Americana**. La sección *Mexicana* se contrasta con la sección *Tanystyloba* y con la sección *Neurocarpum*. La serie *Mexicana* incluye, *C. humilus* Rose, *C. mexicana* Link, *C. monticola* Brandegees, *C. polystachya* Benth. y *C. triflora* Wats. La serie *Tucumania* incluye *C. cordobensis* Burk. La serie *Americana* incluye *C. fragrans* Small y *C. mariana* L. Hay una clave para identificar las especies en la sección *Mexicana*.

Clitoria (Leguminosae) comprises 60 species distributed primarily within the pantropical-subtropical belt, of which 49 species are native to the neotropics. The habit of species of *Clitoria* range from trees, shrubs, lianas, and subshrubs or perennial herbs with erect or twining, annual, aerial stems from an underground xylopodium. It is characterized by its showy, resupinate, papilionaceous flowers, infundibular calyx with persistent bracteoles, and stalked ovaries with a geniculate, bearded style.

Clitoria was last revised by Bentham in 1858. Fantz (1979b) recognized three subgenera circumscribed by fruits and seed morphology, supported by leaf, calyx, androecial, and gynoecial features, germination characteristics, and the presence or absence of cleistogamy. Proposed revisions are based on examination of nine thousand specimens, collected worldwide, that included types.

Fantz (1979a) circumscribed *Clitoria* subg. *Neurocarpum* by its turgid fruit with convex valves (ecostate or bearing a prominent medial nerve), thickened viscid seeds, a subcartilaginous 10-nerved calyx, hypogeal germination, and the presence of cleistogamous flowers in half of its 24 species. Species of subg. *Neurocarpum* have been segregated traditionally by growth form and vegetative characters,

TABLE 1. A COMPARISON OF THE SECTIONS OF SUBGENUS *Neurocarpum*.

Character	<i>Mexicana</i>	<i>Tanystyloba</i>	<i>Neurocarpum</i>
Leaves			
Leaflet number	3-foliolate	3- and 1-foliolate	3- and 1-foliolate
Petiole	Petiolate	Petiolate or subsessile	Petiolate or subsessile
Inflorescence			
Axis length	(1)2-13 cm	0.3-1.5(2) cm	1-10(20) cm
Number per axil	Solitary	Fascicled to solitary	solitary
Chasmogamous flowers			
Flower size	Small, 2.5-4 cm (4-6 cm in <i>C. mariana</i>)	Small, 2.5-4 cm	Medium-large, (3.5)4-7.5 cm
Flower color	White or blue to purple	White	Blue to purple (white)
Calyx tube	Short, 7-12(14) mm	Short, 6-12 mm	Long, 11-22(25) mm
Calyx lobes	Shorter than tube	Longer to subequal tube	Shorter than tube
Staminal tube	Short, 1.3-2.2 cm (2-3 cm in <i>C. mariana</i>)	Short, 1.3-2.2 cm	Long, 2-4 cm
Style	Short, 1-2 cm	Short, 1-1.6 cm	Long, 1.9-3 cm (1.4-1.9 cm in <i>C. falcata</i>)
Cleistogamous flowers			
	Present	Absent	Present
Calyx tube	Small, 3-6 mm		Large, 5-9(11) mm
Calyx lobes	Small, 1.5-3 mm		Long, 3-7 mm
Staminal tube	Elongate, 3-5 mm or nearly lacking, ca. 0.1 mm		Short, 0.5-1.5 mm
Legume and seeds			
Depressed between seed	Weak to strongly	Weakly	Turgid, not depressed
Costa longitudinal	Ecostate	Ecostate	Costate or occasionally ecostate
Seed length/width	Width slightly longer than length	Width slightly longer than length	Length slightly longer than width
Legume width	Narrower, 5-9 mm	Broader, 7-11 mm	Broader, 7-11 mm

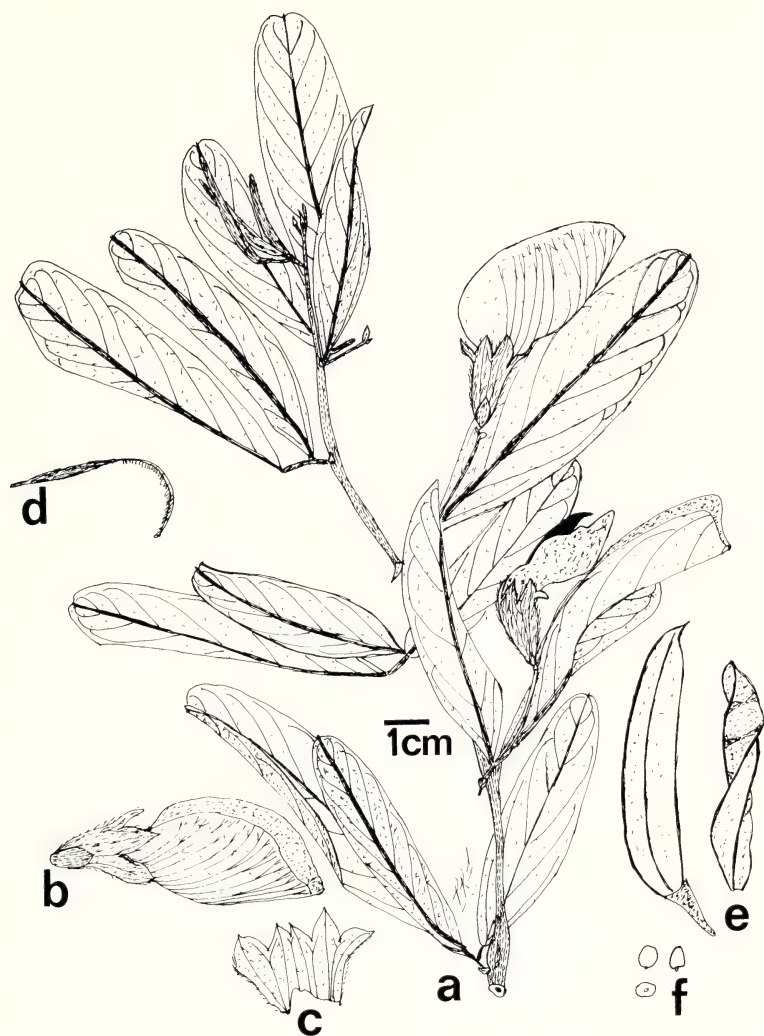


FIG. 1. *Clitoria laurifolia* Poir. (a) aerial stem, $\times 0.5$; (b) flower, $\times 0.5$; (c) calyx, $\times 0.5$; (d) gynoeceium, $\times 0.5$; (e) legumes, $\times 0.5$; (f) three views of seed, $\times 0.5$. (Saltzman s.n., G, a; Smith 2050, GH, b-f.)

e.g., leaflet number, petiole length, and leaflet shape and apices. Fruits and floral characters have been used rarely in floristic treatments or Bentham's (1858) treatise.

There are three sections within subg. *Neurocarpum* as distinguished by a combination of morphological characters and geographical distribution (Table 1). Section *Neurocarpum* (lectotype = *C. laurifolia* Poir., Fig. 1) is a South American group of 10 species with

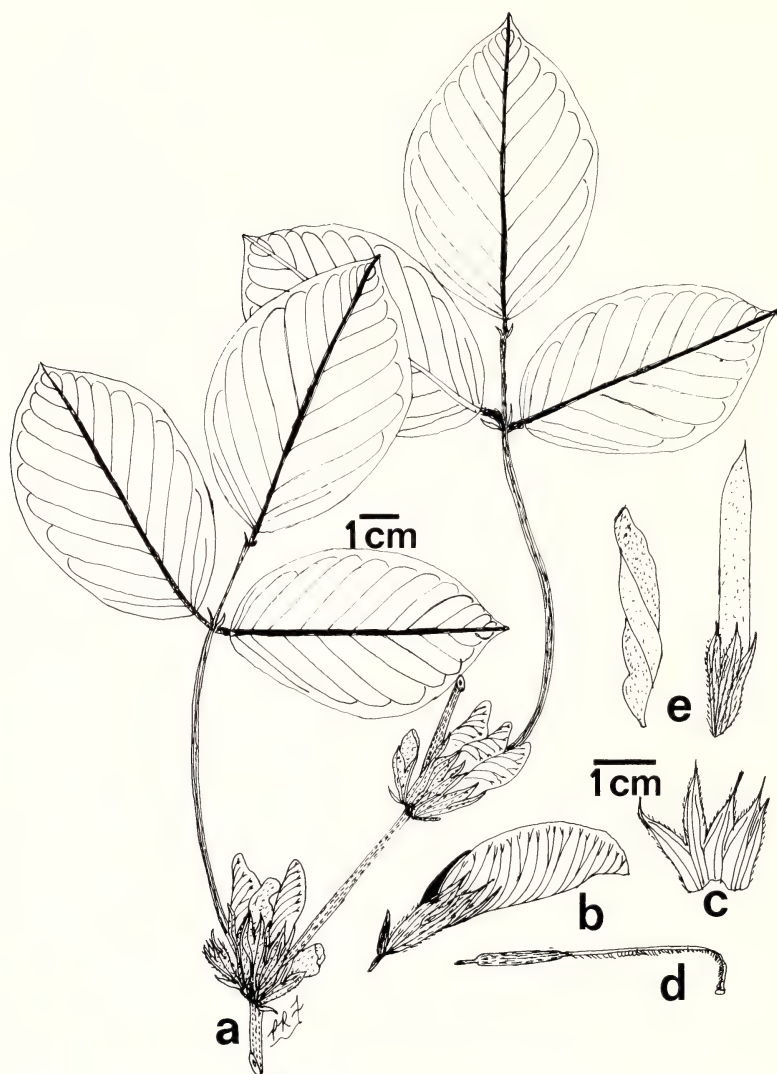


FIG. 2. *Clitoria macrophylla* Wall. ex Benth. (a) portion of stem, $\times 0.5$; (b) flower, $\times 1$; (c) calyx, $\times 1$; (d) gynoeceium, $\times 1$; (e) legumes, $\times 1$. (Wallich 5345, K, a-e.)

three that extend into Central America and the West Indies. Members are characterized by fruits that are turgid, not depressed between the seeds, and often bearing a longitudinal, medial nerve (=costate fruit). Fruits in some species are ecostate or the costa is imperfectly formed. Seeds typically are slightly longer than they are wide (seed length = axis parallel with funiculus). Chasmogamous flowers typ-



FIG. 3. *Clitoria mexicana* Link. (a) portion of stem, $\times 0.5$; (b) flower, $\times 1$; (c) calyx, $\times 1$; (d) gynoecium, $\times 1$; (e) legumes, $\times 1$; (f) three views of seed, $\times 1$. (Breedlove 12025, F, a; Hinton 11668, NY, b; Molina 18472, NY, c, d; Tucker 784, UC, e, f; Hernandez 1287, F, g.)

ically are larger, usually pigmented in shades of blue to purple, or occasionally white. Cleistogamy is present in most species.

Section *Tanystyloba* (type = *C. macrophylla* Wall. ex Benth., Fig. 2) includes five species of Southeast Asia and one endemic in Australia (Fantz, 1979a). Species are unique because they (1) lack cleis-

togamy, (2) bear a calyx with elongated lobes longer than the tube, and (3) possess a dense indumentum of uncinat hairs on the outer calyx surface. Short-petiolate to sessile leaves and occurrence of unifoliate leaves is similar to some species of sect. *Neurocarpum*.

A third group includes seven species from North and Central America and one species native to northern Argentina. These have turgid, ecostate fruits that are depressed between the seeds. Seeds are slightly wider than long. Plants are similar to those of species in sect. *Tanystyloba*, but differ by the presence of cleistogamous flowers, narrower fruits, and elongated inflorescences. These eight species are placed in sect. *Mexicana* (type = *C. mexicana* Link, Fig. 3), a new section of subg. *Neurocarpum*.

TAXONOMIC TREATMENT

Sect. *Mexicana* includes three distinct groups distinguished by morphological differences in fruit and chasmogamous and cleistogamous flowers, supported by geographical distribution. These are treated as Series as described below.

Key to Taxa of sect. *Mexicana*

Floral characteristics, unless otherwise noted, refer to chasmogamous flowers.

1. Gynophore 4–8 mm long, slightly shorter than the ovary; fruits conspicuously depressed between the seeds; staminal tube of cleistogamous flowers nearly lacking, ca. 0.1 mm long, filaments nearly free; flowers blue to lilac to pale purple, (3.5–)4–6 cm long Series *Americana*
2. Calyx tube 7–10 mm long; leaflets narrow, 0.5–1 cm wide, primary nerves of 6–8 pairs; stipules 2–4 mm long, stipels 1–3 mm long; stipe 15–21 mm long; cleistogamous flowers with bracteoles 2–3 mm long, calyx tube 3–4 mm long, stipe 9–14 mm long *C. fragrans*
2. Calyx tube 10–14 mm long; leaflets broad, 1–4(–6.5) cm wide, primary nerves of 7–12 pairs; stipules 5–10 mm long, stipels 3–8 mm long; stipe 5–17 mm long; cleistogamous flowers with bracteoles 3–5 mm long, calyx tube 4–5 mm long, stipe 5–10 mm long *C. mariana*
1. Gynophore 3–4 mm long, much shorter than the ovary; fruits weakly depressed between seeds; staminal tube of cleistogamous flowers elongate, 3–5 mm long; flowers white or pale yellow, occasionally purple, 2.5–4 cm long.
3. Stipe 8–16 mm long, exerted beyond calyx tube; carina with blade 10–11 mm long, claw 18–22 mm; style 8–10 mm long; cleistogamous flowers with staminal tube 3–4 mm long. One species Series *Tucumania* (*C. cordobensis*)

3. Stipe 4–8 mm long, enclosed within calyx; carina with blade 5–9 mm long, claw 12–17 mm long; style 10–17 mm long; cleistogamous flowers with staminal tube 4–5 mm long Series *Mexicana*
4. Flowers 3–4 cm long; calyx lobes 6–8 mm long; inflorescence racemose, 2–4(–6)-flowered; perennial herbs with aerial stems erect to twining.
5. Vine; calyx tube 9–12 mm long, purplish; bracteoles 5–9 mm; inflorescence 2–11 cm long; leaflets ovate to lanceolate; stipules 6–9 mm long *C. mexicana*
5. Erect herb; calyx tube 7–9 mm long, greenish; bracteoles 3–4 mm long; inflorescence 0.2–0.3 cm long; leaflets oblong; stipules 4–6 mm long *C. humilis*
4. Flowers 2.5–3 cm long; calyx lobes 2–5 mm long; inflorescence paniculate (occasionally racemose), 4–8-flowered or more; shrubs to subshrubs.
6. Flowers lilac to purple; calyx lobes 4–5 mm long; stem pubescence spreading; bracteoles 7–9 mm long; cleistogamous flowers not observed *C. triflora*
6. Flowers white; calyx lobes 2–4 mm long; stem pubescence ascending, subappressed; bracteoles 4–7(–9 in variety *C. polystachya*) mm long; cleistogamous flowers present.
7. Inflorescence racemose, few flowered; carina with blade 5–7 mm long; wings with blade 8–11 mm long, claw 10–14 mm long; style 10–11 mm long; ovary moderately uncinatate pubescent; leaflets narrower, 1.5–3.5 cm wide, primary nerves of 3–6 pairs; petiole 3–6 cm long, petiolule 2–3 mm long *C. monticola*
7. Inflorescence paniculate, many-flowered; carina with blade 7–8 mm long; wings with blade 12–14 mm long, claw 8–11 mm long; leaflets broader, 2–6 cm wide, primary nerves of 8–12 pairs; petiole 4–10 cm long, petiolule 3–5 mm long *C. polystachya*

Clitoria L. subgenus **Neurocarpum** (Desv.) Baker sect. **Mexicana** Fantz, sect. nov.

Sectione nova *Clitoria* subgenere *Neurocarpum* cum *Tanystyloba* affini optimo distinguitur a inflorescentia solitario et elongato, calyce lobis breviores longi tubo et flores cleistogamis praesentia.

Leaves 3-foliolate, petiolate. Inflorescences axillary, solitary, paniculate or racemose, (1–)2–several flowered; peduncles 2–13 cm long. Chasmogamous flowers showy, white or blue to purple, 2.5–4(–6) cm long. Calyx tube 7–12(–14) mm long; lobes shorter than

the tube; sparingly to moderately pubescent with uncinat trichomes and subappressed macroscopic trichomes. Staminal tube 1.3–2.2(–3) cm long. Style 1–2 cm long. Cleistogamous flowers inconspicuous, 0.4–0.9 cm long. Calyx tube 3–6 mm long; lobes 1.5–3 mm long. Staminal tube elongate, 3–5 mm long, or ca. 0.1 mm long. Legume ecostate, valves weakly to strongly depressed between seeds.

Sp. typica: *Clitoria mexicana* Link.

Members of sect. *Mexicana* typically occur in dry sandy soils, often in drier woodlands of lowlands and mountain slopes to about 2700 m. Three distinct series are observed.

1. Series **Mexicana**

Shrubs, subshrubs to suffrutescent herbs. Chasmogamous flowers 2.5–4 cm long, white fading pale yellow, or occasionally purplish; gynophore 3–4 mm long, much shorter than the ovary; style 10–17 mm long. Cleistogamous flowers with staminal tube 3–5 mm long. Legume weakly depressed between the seeds, short-stipitate; stipe 4–8 mm long; seeds slightly wider than long. Central America.

Series *Mexicana* includes the following species: *C. humilus* Rose, Mexico (holotype: *Rose 2251*, US!), *C. mexicana* Link, Mexico to Nicaragua (neotype: *Hinton 11668*, NY!), *C. monticola* Brand., Mexico (holotype: *Brandeggee s.n.*, UC 83907!), *C. polystachya* Benth., Mexico to Panama (lectotype: *Hartweg 454*, K!), and *C. triflora* Wats., Mexico (lectotype: *Palmer 159*, GH!). These species are postulated to have originated in Mexico with two species migrating into Central America. Wiggins (1980) omitted *C. monticola* from the flora of Baja California.

2. Series **Tucumania** Fantz, ser. nov.

Serie nova *Mexicana* optimo distinguitur a stipite elongato, carino longiores, stylis breviores, et tubo staminali e flores cleistogamis breviores. Tucumania.

Perennial suffrutescent herbs. Chasmogamous flowers 2.5–3 cm long, white; gynophore 3–4 mm, much shorter than the ovary; style 5–6 mm long. Cleistogamous flowers with staminal tube 3–4 mm long. Legume long-stipitate, valves weakly depressed between the seeds; stipe 10–16 mm long; seeds slightly wider than long. Argentina.

Sp. typica: *Clitoria cordobensis* Burkart.

Clitoria cordobensis, endemic to northern Argentina (lectotype: *Nicora 1774*, SI!), is the only member of this series.

3. Series **Americana** Fantz, ser. nov.

Serie nova *Mexicana* optimo distinguitur a gynophoro elongato fere subequalis ovario, flores statura ampliore, et tubo staminali e

flores cleistogamis brevissimo. Americana cum orientalis disjuncto varieto.

Perennial suffrutescent herbs. Chasmogamous flowers 3.5–6 cm, bluish to lilac to pale purple; gynophore 4–8 mm long, slightly shorter than the ovary; style 13–20 mm long. Cleistogamous flowers with the staminal tube ca. 0.1 mm long, the stamens appearing to be free. Legumes conspicuously depressed between the seeds, long-stipitate; stipe 10–21 mm long; seeds slightly longer than wide. United States (one variety in se. Asia).

Sp. typica: *Clitoria mariana* L.

Series *Mariana* includes two species, *C. mariana* L., from the U.S. with a variety in Southeast Asia (type: *Hb. Petiver*, BM—Hb. Sloane) and *C. fragrans*, an endemic to southern Florida (lectotype: *Small and Wherry 12626*, NY!).

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MORPHOLOGICAL AND ECOLOGICAL VARIATION
ACROSS A HYBRID ZONE BETWEEN
ERYTHRONIUM OREGONUM AND
E. REVOLUTUM (LILIACEAE)

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ABSTRACT

Erythronium oregonum and *E. revolutum* overlap only slightly in geographic distribution, but can hybridize where they co-occur. Morphological traits of *Erythronium* and cover of associated species were assessed in 1m² plots in one hybrid and several pure populations of these two species on Vancouver Island. The species differ in size of flowers, relative size of scape and leaves, and several flower color characters. They also differ ecologically, *E. oregonum* occupying drier microsites than *E. revolutum*. Hybrids between them exhibited various recombinations of the parental morphological traits. Morphological variation in *Erythronium* at the hybrid locality was correlated with the ecological characteristics of the plots as indicated by a detrended correspondence analysis of associated plant species ($r = 0.64$). *Erythronium oregonum* and *E. revolutum* apparently are maintained as separate taxa by their ecological differences.

The genus *Erythronium* reaches its greatest diversity in western North America, where approximately 14 species occur (Applegate 1935, Hitchcock et al. 1969, Hammond and Chambers 1985). Although some of these have been studied ecologically (Caldwell 1969, Antos and Zobel 1984, Thomson and Stratton 1985), little is known about evolutionary relationships within the genus, or the genetic and ecological basis for species differences.

Erythronium oregonum Applegate and *E. revolutum* Smith are lowland species of the Pacific Northwest. They are morphologically and ecologically similar, and Applegate (1935) has reported hybrids between them. Both species have mottled leaves, small saccate appendages on the inner tepals, dilated anther filaments, and a three-lobed stigma. *Erythronium revolutum* has yellow anthers and rose pink tepals with yellow banding at the base. *Erythronium oregonum* is more variable; in many populations (including those in British Columbia) the anthers are yellow and the tepals are white with yellow and red banding at the base, but southern populations commonly have paler anthers and cream-colored tepals lacking the red markings. In this paper we describe an instance of hybridization between *E. oregonum* and *E. revolutum* in British Columbia, and present evidence concerning morphological and ecological differences between the two species.

METHODS

Study plots. Hybrids occurred with *E. oregonum* and *E. revolutum* at Skutz Creek (48°47'N, 123°57'W), a small tributary of the Cowichan River located 9.2 km east of Cowichan Lake on southern Vancouver Island, British Columbia. We established 29 1 m² plots at this site in areas of high *Erythronium* density. The plots were located to encompass the full range of variation in morphology and habitat of *Erythronium* at the site. For comparison, we located eight additional plots in pure populations of *E. oregonum*, of which five were along the Cowichan River (1.0 km downriver from Skutz Creek, 48°47'N, 123°56'W) and three were near Victoria (at Beaver Lake, 48°31'N, 123°23'W, and on the University of Victoria campus, 48°28'N, 123°19'W). We also located five plots in pure populations of *E. revolutum* along Sutton Creek (48°49'N, 124°13'W), 2.0 km west of Honeymoon Bay on Cowichan Lake.

Morphological characteristics. We measured eight morphological characters of taxonomic importance (tepal color, style color, stamen filament color, intensity of red banding on tepals, tepal length, length of dehiscent anthers, scape height, and leaf length) on 25 plants in each of the 42 plots. Only characters that could be assessed non-destructively were used. Color intensities (hue and lightness) were determined using a Munsell color chart (Munsell Color, Baltimore, MD). We also calculated a derived character, scape-leaf ratio (=scape length/leaf length).

We used pure populations of *E. oregonum* and *E. revolutum* to establish mean values of the diagnostic characters of each species. The Cowichan River and Victoria populations of *E. oregonum* were not significantly different (t-test for each character, $p > 0.05$ in all cases), so the data from these were combined. We constructed a hybrid index using six characters (tepal color, style color, filament color, red banding, tepal length, and scape-leaf ratio) that differed significantly between the two species, but were not highly correlated with other characters. For all plants examined at the Skutz Creek hybrid locality, the values of each character were scaled between the mean values for *E. revolutum* (set at zero) and for *E. oregonum* (set at 10). Values outside the range of zero to 10 were set to zero or 10 as appropriate. A weighting factor inversely related to the amount of overlap between the pure populations was then applied to each character (weights were 1.000 for tepal color, 0.984 for style color, 0.887 for filament color, 0.930 for red markings, 0.720 for tepal length, and 0.645 for scape-leaf ratio). The hybrid index was calculated as the sum of these weighted values for the individual characters, and this sum was then scaled between zero and 60. We calculated a mean hybrid index for each plot in order to determine

TABLE 1. MEAN VALUES OF CHARACTERS USED IN STUDY OF *Erythronium oregonum* AND *E. revolutum*. Color traits are expressed as values on an integer scale; tepal, style, and filament color vary from 0 (white) to 7 (deep violet-pink), and red banding from 0 (absent) to 5 (broad deep-red bands). All characters differed significantly between the two species (t-test; p values given below).

Character	<i>E. oregonum</i> (n = 200)		<i>E. revolutum</i> (n = 125)		p
	\bar{x}	s.d.	\bar{x}	s.d.	
Tepal color	0.0	0.1	4.6	0.5	0.0001
Style color	0.0	0.0	3.4	1.3	0.0001
Filament color	0.2	0.9	3.7	1.8	0.0001
Red banding	2.2	1.2	0.0	0.0	0.0001
Anther length (mm)	6.6	1.1	6.2	0.9	0.0003
Petal length (mm)	44.7	5.0	37.0	2.9	0.0001
Leaf length (cm)	16.9	4.3	16.1	2.3	0.0253
Scape height (cm)	28.0	7.1	21.4	2.9	0.0001
Scape-leaf ratio	1.7	0.2	1.3	0.1	0.0001

whether plants in the plot were predominantly “*revolutum*”, “*oregonum*” or “hybrid” in character.

Ecological characteristics. For all 1 m² plots except those at Victoria, we recorded the percent cover of each vascular plant and moss species present. All cover values were subjected to log transformation before analysis. We carried out detrended correspondence analyses of these data using the program DECORANA (Hill 1979) in order to assess ecological resemblance among the plots. The analyses were performed with all plots and with the Skutz Creek plots only, with and without tree species included. We then examined the relationship between *Erythronium* morphology, as indicated by the hybrid index, and ecological characteristics, as indicated by plot ordination scores derived from the detrended correspondence analysis.

RESULTS

Morphological characteristics. Populations of *E. oregonum* and *E. revolutum* differed in a number of the morphological characters examined (Table 1). The most striking differences between the two species are in tepal color and markings. Other differences, which were observed during this study but not measured, included (1) length of stigma lobes (shorter in *E. revolutum*); (2) curvature of tepals (much reflexed in *E. revolutum*, generally less so in *E. oregonum*); (3) anther position (connivent around the style in *E. revolutum*, spreading in *E. oregonum*); and (4) leaf position (generally more erect in *E. revolutum*).

We examined correlations among the characters in Table 1, first for all of the specimens measured at the Skutz Creek locality, and

TABLE 2. PERCENT COVER AND (IN PARENTHESES) PERCENT OCCURRENCE OF VASCULAR PLANT SPECIES IN PLOTS GROUPED BY THE *Erythronium* HYBRID INDEX. Included are all species with >5% cover in at least one group. T = <0.5% cover; nomenclature follows Hitchcock and Cronquist (1973).

Species	Hybrid Index		
	<10 (n = 6)	10-50 (n = 16)	>50 (n = 7)
Trees			
<i>Alnus rubra</i>	78 (100)	50 (94)	16 (57)
<i>Abies grandis</i>	2 (17)	8 (50)	0 (0)
<i>Acer macrophyllum</i>	11 (100)	27 (100)	29 (57)
<i>Pseudotsuga menziesii</i>	10 (17)	1 (19)	42 (86)
Shrubs			
<i>Rubus spectabilis</i>	32 (83)	22 (81)	1 (14)
<i>Oemleria cerasiformis</i>	8 (67)	9 (69)	11 (29)
<i>Symphoricarpos albus</i>	0 (0)	5 (31)	7 (43)
<i>Holodiscus discolor</i>	T (17)	T (6)	37 (57)
Herbs			
<i>Trautvetteria caroliniensis</i>	32 (83)	5 (38)	T (14)
<i>Maianthemum dilatatum</i>	13 (33)	10 (38)	1 (14)
<i>Dicentra formosa</i>	7 (33)	6 (50)	1 (14)
<i>Tolmiea menziesii</i>	2 (50)	13 (56)	T (14)
<i>Heracleum lanatum</i>	4 (50)	9 (31)	6 (29)
<i>Viola glabella</i>	T (17)	6 (50)	8 (43)
<i>Cardamine pulcherrima</i>	3 (17)	4 (38)	16 (86)
<i>Perideridia gairdneri</i>	0 (0)	0 (0)	9 (43)

secondly for that subset of specimens with a hybrid index between 20 and 40. In the first comparison some high correlations occurred between characters found together in the same species, particularly color characters. The highest correlation coefficient (0.78) was between tepal color and filament color. In the second comparison, which was restricted to clearly hybrid specimens, no correlation coefficient higher than 0.51 was obtained, and most were much lower.

Ecological characteristics. Results of the detrended correspondence analyses indicate that *E. oregonum* and *E. revolutum* differ in their ecological characteristics. The ordinations were all similar and the first axis in each case corresponded to a moisture gradient. At the hybrid locality typical *E. oregonum* was usually found on well-drained microsites underlain with shale, whereas typical *E. revolutum* was usually found on wetter microsites with black, humus-rich soils. Sample plots grouped on the basis of mean hybrid index into "oregonum", "revolutum" or "hybrid" differed substantially in species composition (Table 2). *Erythronium oregonum* typically grew in sites with a Douglas-fir canopy and sparse herbaceous understory;

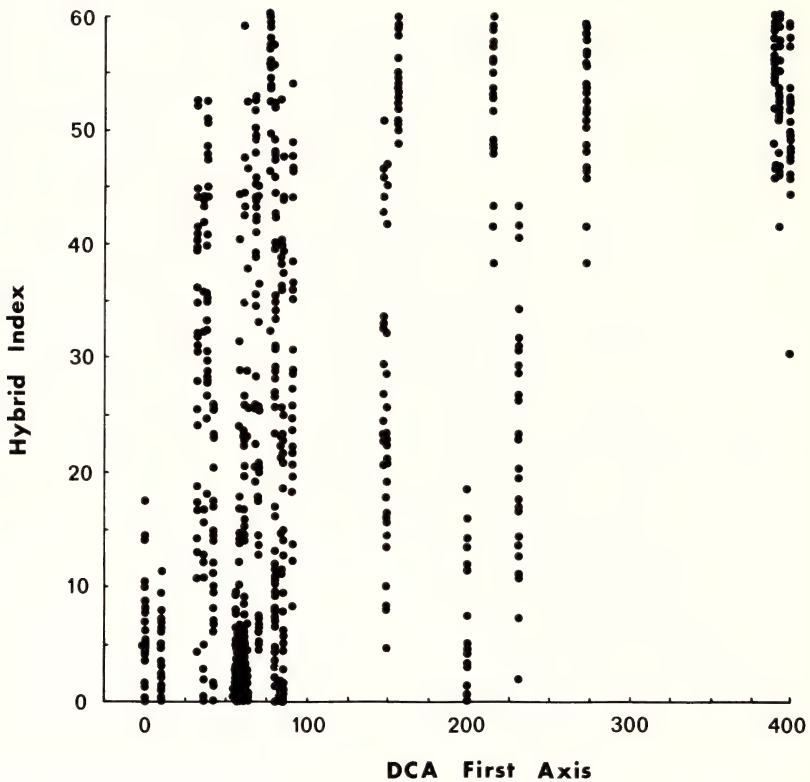


FIG. 1. Hybrid index of individual *Erythronium* in relation to their position on the first axis of a detrended correspondence analysis (DCA) of the 29 plots at Skutz Creek. The analysis was based on all associated species. Low scores on the DCA axis correspond to wetter sites and high scores to drier sites; typical *E. revolutum* has a hybrid index of zero, and typical *E. oregonum* a hybrid index of 60.

in contrast, *E. revolutum* was typically associated with luxuriant herb layers under a red alder canopy.

To examine relationships between morphological and ecological characteristics of *E. oregonum*, *E. revolutum* and their hybrids, we plotted the hybrid indices of all plants from the Skutz Creek locality against plot scores from the first axis of the detrended correspondence analysis (Fig. 1). The first DCA axis accounted for 57% of the variation in the species composition of the sample plots, and corresponded roughly to a moisture gradient with low scores indicating wetter sites and high scores indicating dry sites. Plots with low scores on the first DCA axis contained mainly *E. revolutum*, and those with high scores on this axis contained mainly *E. oregonum* (Fig. 1). The large amount of scatter in the central region of the figure indicates that *E. oregonum* and *E. revolutum* overlapped slightly in

their ecological tolerances, and also that the hybrid plants at Skutz Creek exhibited many combinations of morphological and ecological characteristics. Although the morphology of *Erythronium* plants varied greatly in plots located in intermediate habitat, 41% of the variation in mean hybrid index was related to position on the first DCA axis.

DISCUSSION

The western North American species of *Erythronium* are largely allopatric in their distribution, and little quantitative information exists concerning the degree of interfertility and naturally occurring intergradation among species. Although only a few cases of hybridization between *E. oregonum* and *E. revolutum* have been reported (Applegate 1935), extensive hybridization can occur under appropriate conditions. The variety and abundance of intermediate forms found at the Skutz Falls study site suggest that many hybrid generations are present and that there is little or no post-zygotic reproductive isolation between the species, at least at this locality. Applegate (1935) considered these two species to be related closely on morphological grounds. Nevertheless, *E. oregonum* and *E. revolutum* are consistently different in a number of morphological characters as well as in their ecological requirements.

The evidence presented in this paper suggests that *E. oregonum* and *E. revolutum* maintain their distinct taxonomic characteristics largely through ecological separation. On Vancouver Island, *E. revolutum* typically occurs under deciduous trees on relatively wet sites such as stream terraces. It can be abundant, locally dominating the herb layer, but occurs on a restricted range of sites. *Erythronium oregonum* is most common on dry open sites such as forest openings and rock outcrops, although it occasionally occurs in wetter locations; it appears to occupy a wider variety of sites than *E. revolutum*. The overall geographic distributions of the two species reflect these ecological differences. *Erythronium revolutum* occurs on Vancouver Island and the adjacent mainland to the north, then south through the Olympic Peninsula of Washington and coastal regions of Oregon to northern California (Bierly and Stockhouse 1982, James 1983). Its occurrence is somewhat sporadic, probably reflecting relatively specific habitat requirements and the patchy distribution of suitable sites. *Erythronium oregonum* extends from the east coast of Vancouver Island and adjacent mainland British Columbia, southward through the Puget Trough of Washington and the Willamette Valley of Oregon (extending into the Coast Range and to the west slope of the Cascades); it reaches its southern limit in the vicinity of the Illinois River of southern Oregon (Applegate 1935).

Although the two species exhibit some overlap in range, they

seldom grow in close proximity because of their differences in habitat preference. For successful hybridization to occur, pollen or seeds must be transferred between parental populations. In *Erythronium*, this seems likely only if the two taxa are established immediately adjacent to one another. Such a situation exists at Skutz Creek, where dry slopes with fairly pure *E. oregonum* populations occur within 100 m of alluvial flats with populations of *E. revolutum*. Given the apparent absence of intrinsic genetic barriers between these two species, the close juxtaposition of divergent habitats that can support both taxa is probably the major reason for hybridization.

ACKNOWLEDGMENT

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CROSSABILITY AND RELATIONSHIPS OF *PINUS MURICATA* (PINACEAE)

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ABSTRACT

Crossing relationships were studied within and among the variable populations of *Pinus muricata* to test hypotheses about crossing barriers among certain populations. Crossability was assessed at the level of viable seed production following planned crosses. Populations north of Sea Ranch, Sonoma Co., California, crossed freely with parapatric but genetically distinct populations in central Sonoma Co., although some reduction in seed-set occurred in the F_2 and backcrosses to F_1 . The distinctness of these adjacent populations is most likely not maintained by post-pollination crossing barriers. Crossability of disjunct *P. muricata* populations generally decreased with distance between populations. Populations north of Sea Ranch crossed freely with the Pt. Reyes population in Marin Co., less readily with the Monterey population, and not at all with the Purisima (southern California) or Baja California populations. Mainland and island *P. muricata* populations south of Monterey were highly interfertile. Test crosses were also attempted between *P. muricata* and the island populations of *P. radiata*, which have been considered closely related to southern *P. muricata* populations. *Pinus muricata* from Baja California did not cross, however, with either Guadalupe Island pine (*P. radiata* var. *binata*) or Cedros Island pine (*P. radiata* var. *cedrosensis*). Together with results from other crossing studies in the Californian closed-cone pines, the patterns of crossability indicate three crossing units in *P. muricata*: 1) northern *P. muricata* populations from Marin Co. northward, which are reproductively isolated from, 2) southern *P. muricata* populations including mainland and Channel Islands populations from Purisima southward, and 3) Monterey *P. muricata*, which is intermediate between the first two units.

Crossing patterns within the three Californian species of closed-cone pines (subsect. *Oocarpae*, Critchfield and Little 1966) are unusual for *Pinus*. In experimental pollinations, *Pinus radiata* D. Don and *P. attenuata* Lemmon hybridize more readily than most other combinations in the genus, whereas crosses between certain northern and southern populations of *P. muricata* D. Don do not produce viable seeds (Critchfield 1967). This is the only known instance in *Pinus* of complete infertility between populations within a species.

Pinus muricata is unique among the California closed-cone pines because of the distribution of genetic variation within and among

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populations. The frequencies of several morphological and biochemical traits in northern populations of *P. muricata* change abruptly within continuous stands. Cone morphology in southern populations also differs markedly within and among nearby disjunct stands. Variation is especially complex in the southern and island populations where several traits intergrade between *P. muricata* and *P. radiata*.

This variation has led taxonomists since the early 1800's to apply many species and varietal names to populations and morphological types in these taxa (Millar 1986). It also has led them to explain the origins and relationships of populations with often contradictory hypotheses. Early botanists focused on, and paleontologists still rely on, seed-cone observations in making evolutionary inferences about the closed-cone pines. Observations of other traits often have led to conflicting interpretations. In this paper, we focus on crossability, a measure of genetic relatedness that estimates the potential for gene exchange among taxa. We use this measure to test several hypotheses about relationships among the populations of *P. muricata*. In particular, we consider the hypotheses that genetic distinctness among parapatric races of *P. muricata* in northern California is maintained by crossing barriers, that Monterey *P. muricata* crosses more readily with northern than with southern populations, that *P. muricata* populations at Purisima cross more readily with southern than with northern populations, and that southern *P. muricata* populations are isolated reproductively from the island populations of *P. radiata*.

VARIATION AND HYBRIDIZATION

Variation in Pinus muricata. The three Californian species of subsect. *Oocarpae* are separated from the four taxa restricted to Mexico and Central America by a 640 km gap (Critchfield and Little 1966). The northern group includes *P. attenuata*, a montane, interior element, and *P. muricata* and *P. radiata*, which are maritime/insular elements (Fig. 1; Griffin and Critchfield 1976). Whereas *P. attenuata* ranges widely in southern Oregon, California, and Baja California, *P. radiata* is limited to three mainland populations in California (Año Nuevo, Monterey, and Cambria) and two distinct island populations in Mexico (Cedros and Guadalupe Islands).

Pinus muricata comprises nine disjunct populations that extend from Trinidad in northern California to San Vicente in northern Baja California and to two of the Channel Islands, Santa Cruz and Santa Rosa (Fig. 1). Of the three closed-cone pine species, *P. muricata* has the most interpopulation variability (Fielding 1961, Doran 1974, Millar et al. 1987). Both discontinuous and clinal patterns of variation occur (Millar 1986, Millar et al. 1987). Populations north of Monterey (*P. muricata* var. *borealis*, Axelrod 1983) are distinct in growth and form from the highly variable southern populations

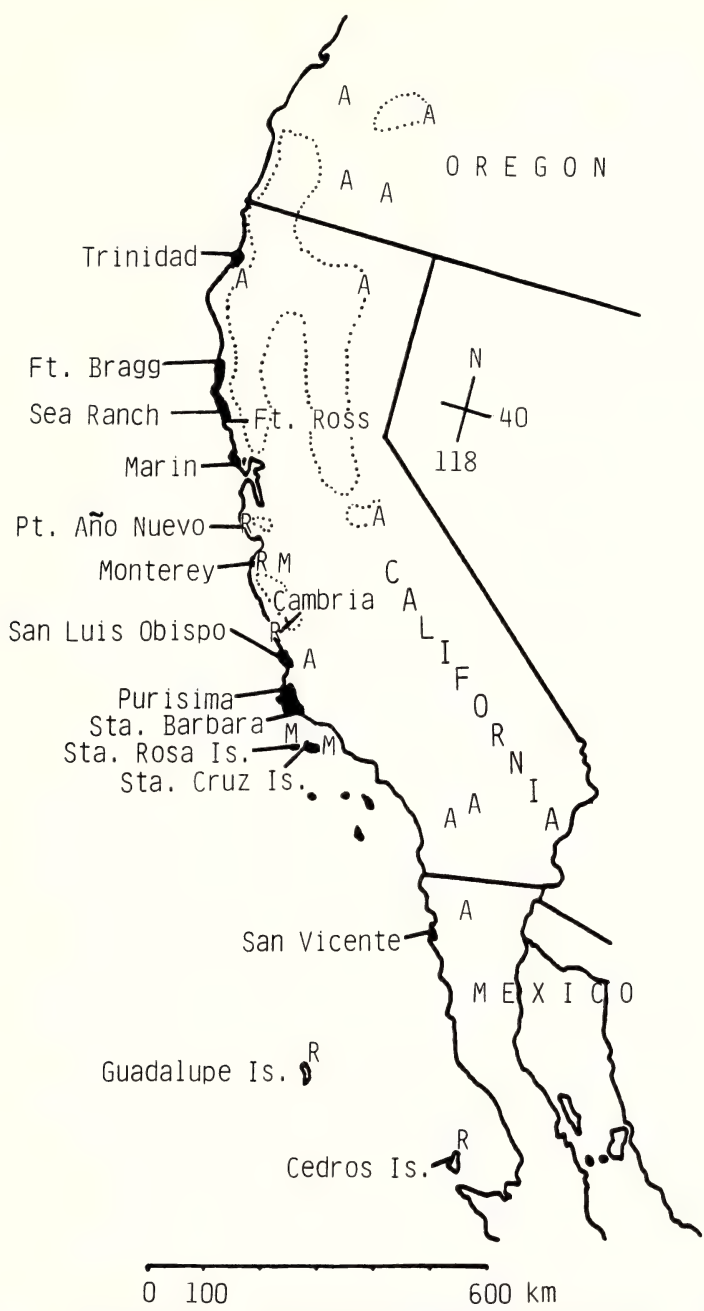


FIG. 1. Distribution of *P. muricata* (shaded areas and areas marked M), *P. radiata* (areas marked with R), and *P. attenuata* (enclosed with dotted lines and areas marked with A) in California and Baja California.

TABLE 1. VARIATION IN *Pinus muricata* POPULATIONS: STOMATAL ANATOMY, MONOTERPENE COMPOSITIONS, GROWTH AND FORM, CONE SHAPE, AND RESIN CANAL NUMBER. ¹Blue = open, wax-filled epistomatal chambers, green = partly closed, waxless chambers, Duffield 1951. ²Mirov et al. 1966. ³Composite rank from common-garden studies, including height growth, stem volume, stem straightness, and bark roughness. Rank 1 = greatest height, volume, straightest stem, and roughest bark, Duffield 1951, Fielding 1961, Shelbourne 1974, Shelbourne et al. 1982. ⁴1 = populations with mostly armed, asymmetric cones, 2 = populations with mostly smooth, symmetric cones, 3 = populations with many cone types, Mason 1930, Duffield 1951, Axelrod 1980, 1983, pers. observ. by authors. ⁵Unpublished data by authors except references noted. ⁶Averages of trees within populations with armed and unarmed cones. ⁷Duffield 1951. ⁸Linhart et al. 1967.

Population	Stomatal type ¹	Monoterpene composition ²	Growth & form ³	Cone shape ⁴	Mean no. resin canals ⁵		
					All types	Armed cones ⁶	Unarmed cones ⁶
Trinidad, Humboldt Co.	blue	>98% α -pinene	1-2	1	2.0		
Mendocino Co.	blue	>98% α -pinene	1	1	2.3 ⁷		
		>80% Δ -3-carene			2.6		
Sonoma Co.	green		1	1	1.8		
Marin Co.							
Pt. Reyes Inland	green	>80% Δ -3-carene	2	3	2.1	2.2	2.0
	green			3	2.1		
Monterey Co.	green	>80% Δ -3-carene	3	3	3.2	3.2	3.1
San Luis Obispo Co.	green	>75% sabinene & terpinolene	4	3	4.1 ⁸		
Purisima, Santa Barbara Co.	green	>75% sabinene & terpinolene	4	3, 2	4.1 ⁷		
					3.9 ⁸		
Santa Cruz Island	green	>85% α -, β -pinene, sabinene, & terpinolene	5	3, 2	6.8 ⁸	7.5 ⁸	6.1 ⁸
Santa Rosa Island	green	>90% α -, β -pinene, sabinene, & terpinolene	6	2	4.4 ⁸		4.4
San Vicente, Baja CA	green	>75% sabinene & terpinolene	5	3, 2	7.0 ⁷		
					8.6 ⁸		
					7.4	8.0	6.8

(Table 1; Duffield 1951). *Pinus muricata* var. *borealis* is further divided into two discrete genetic races that are separated by a narrow contact zone at Sea Ranch, Sonoma Co., California. The races are distinguished by needle anatomy (Duffield 1951), monoterpene composition (Mirov et al. 1966), phenology, and isozymes (Table 1; Millar 1983). The northern race has foliage that appears blue due to open, wax-filled epistomatal chambers. In this paper we follow the convention of calling all populations with this stomatal type, "blue *P. muricata*". The blue populations also have a distinct terpene composition (Mirov et al. 1966). The partly closed, wax-free epistomatal chambers of the southern race of var. *borealis* and all other *P. muricata* populations southward give the foliage a yellow-green color, here called "green *P. muricata*". Although the green needle anatomy is typical of all populations south of Sea Ranch, the terpene composition found in the green populations immediately south of Sea Ranch occurs elsewhere only in the Monterey population of *P. muricata* (Mirov et al. 1966). The highly variable southern mainland populations (*P. muricata* var. *muricata*) form a third distinct terpene type, whereas the island populations form a fourth terpene type (Table 1). The island pines, variously designated as *P. remorata* (Mason 1930), *P. muricata* var. *remorata* (Duffield 1951), or *P. muricata* f. *remorata* (Hoover 1966), have high frequencies of a deviant cone type (symmetric cones with smooth apophyses) that also occurs in the central and southern mainland populations (Table 1).

Previous reports of hybridization. Natural hybrids between *P. muricata* and *P. radiata* have been reported at Monterey, which is the only place they are sympatric (Mason 1949, Stebbins 1950, Duffield 1951). Lack of intermediates, however, in quantitative traits (Forde 1964) and terpene compositions (Bannister et al. 1962, Forde and Blight 1964), differences in phenology (Duffield 1953, Critchfield 1967), and low crossability of *P. muricata* and *P. radiata* (Critchfield 1967) make this hybridization seem unlikely.

Brown (1966) and Critchfield (1967) studied interfertility among certain populations of closed-cone pines. Using relative numbers of viable seed produced among experimental crosses, they concluded that *P. muricata* consists of three crossing groups: 1) a northern, divergent group, that is isolated from related species and from southern *P. muricata* populations; 2) a southern group that is able to cross with related species; and 3) a central group that is intermediate in crossing relationships. It is noteworthy that all interpopulation crosses in *P. muricata* between northern blue populations and green populations south of Monterey failed. The geographically intermediate population at Monterey crossed poorly with the southern populations, and more readily with the northern blue populations. Crosses

TABLE 2. PARENT TREES OF *Pinus muricata* AND *P. radiata* CROSSES MADE IN NATIVE POPULATIONS AND IN PLANTATIONS AT THE INSTITUTE OF FOREST GENETICS AND RUSSELL RESERVATION.

Race or taxon	Geographic origin	Number of parents	
		Females	Males
1. Native populations			
Blue bishop	Mendocino Co.	—	4
	Sonoma Co.	3	2
Green bishop	Sonoma Co.	4	10
	Marin Co.	—	3
	Monterey	—	2
	Purisima	—	3
2. Plantations			
Russell Reservation (Lafayette, CA)			
Blue bishop	Mendocino Co.	8	15
Green bishop	Sonoma Co.	10	13
Institute of Forest Genetics (Placerville, CA)			
Blue bishop	Mendocino Co.	3	3
Green bishop	Monterey	1	—
	Santa Cruz Is.	1	—
	Santa Rosa Is.	—	1
	San Vicente	3	2
Blue × green bishop (F ₁)	Mendocino & Marin cos., Monterey	4	4
Monterey pine	Guadalupe Is.	—	—
	Cedros Is.	—	1

between trees from contiguous blue and green stands were not included in studies by Critchfield (1967) or Brown (1966).

All crosses attempted by Critchfield and Brown failed between blue *P. muricata* and either *P. attenuata* or *P. radiata*. By contrast, *P. muricata* from Monterey set some sound seeds in combinations with mainland *P. radiata* and *P. attenuata*, whereas Channel Islands *P. muricata* produced many sound seeds in those combinations. *Pinus muricata* from San Vicente produced moderate amounts of viable seed in combination with *P. attenuata*, but none with mainland *P. radiata*, and few with *P. radiata* from Guadalupe Island.

MATERIALS AND METHODS

Parent trees. Crosses on *P. muricata* were made during two periods and in three places (Table 2). In 1965–66 crosses were made on blue and green trees in native stands near Sea Ranch. In the same years, pollen parents from several native stands were crossed with females of different origins planted at the Institute of Forest Genetics (IFG), Placerville, California (elev. 825 m). In 1980–81 crosses were made at IFG on a single blue tree and on four blue × green hybrids. The

hybrids had originated from 1965 crosses and were planted in 1968. Although the trees grew poorly, by 1980 they had been sexually mature for several years. Crosses in 1980–81 also were made on 13- and 14-year-old trees growing in a common-garden plantation at the Russell Reservation, Univ. of California, 16 km east of Berkeley. *Pinus muricata* grows well there, and the trees had been sexually mature for several years prior to pollination.

Pollen for the 1965–66 pollinations was collected from arboretum and native-grown trees, and stored frozen for a year before use. Fresh pollen from plantation trees was used for the 1980–81 crosses.

Breeding techniques and terminology. Trees were pollinated and seeds processed using standard techniques (Cumming and Righter 1948). Seeds from 1965–66 pollinations were sorted using a Clipper mill. If less than 10 viable seeds per cone remained, they were x-rayed to determine viability. Viable seed yields from 1980–81 crosses were determined by germination of all harvested seeds. Crosses that failed to yield cones or had severely insect-damaged cones were excluded from analyses.

An **attempt** in this study refers to the pollination in a single season of a single female parent with pollen from a particular pollen source. All but one set of crosses in this study were single-pair matings with only one male parent contributing pollen. In these matings, the number of attempts for a given cross also specifies the number of male and female parents. In the single cross where a pollen mix was used (San Vicente \times San Vicente, pollen mix of two males), each attempt involved three parents: one female and these two males.

Crossability refers to the ease with which two taxa can be successfully crossed, compared to control crosses within the maternal taxon. For accurate estimation of crossability, it is essential to compare between-taxon crosses to within-taxon control crosses, since the amount of viable seed naturally produced within taxa varies. Controls reported here for each cross combine results from control crosses involving the same female used in the interpopulation crosses, and control crosses on other females of the maternal taxon. We quantify crossability as the number of viable seeds per cone produced from between-taxon crosses expressed as a percent of the number of viable seeds from the within-taxon control crosses. Thus, percents less than 100 indicate fewer viable seed produced from between- than within-taxon control crosses, percents equal to 100 indicate an equal number from each type of cross, and percents greater than 100 indicate more viable seed produced from between- than within-taxon crosses. Differences in numbers of viable seeds among crosses were tested by analysis of variance with significant differences reported for p values less than 0.05. Differences among crosses in germination of seeds were tested by chi-square analyses, with the same significance level.

TABLE 3. SUMMARY OF CROSSES BETWEEN BLUE AND GREEN *Pinus muricata* POPULATIONS (PARENTS FROM MENDOCINO AND SONOMA COUNTIES) MADE ON NATIVE AND PLANTATION TREES. ¹CI = 95% confidence interval, based on average results per attempt, not per cone. ²Expressed as average percent of total number of seeds/cone that germinated. ³The F₁'s in all cases are blue-female/green-male combinations.

Parents		Attempts	Attempts producing sound seeds	Female strobili pollinated	Percent of strobili producing cones	Total number of seeds/cone		Number of viable seeds/cone		Germi- nable seed (%) ²
Females	Males					Mean	CI ¹	Mean	CI ¹	
I. Native populations										
Interpopulation crosses:										
Green	Blue	3	1	16	18.8	29.0	—	24.0	—	82.8
Blue	Green	10	8	101	37.4	75.1	(5.1)	64.8	(5.5)	87.2
Within-population crosses:										
Blue	Blue	6	6	50	60.0	61.0	(7.7)	48.3	(6.9)	81.2
II. Russell Reservation										
Interpopulation crosses:										
Green	Blue	19	15	68	79.4	12.9	(3.5)	5.7	(2.1)	44.8
Blue	F ₁	7	5	17	76.5	14.7	(10.3)	8.4	(9.1)	52.6
Green	F ₁	10	6	22	86.4	10.1	(3.3)	5.7	(2.5)	51.0
Within-population crosses:										
Green	Green	18	10	43	86.0	17.3	(5.0)	8.2	(2.5)	46.3
Blue	Blue	6	6	33	75.8	5.3	(0.9)	1.1	(0.5)	31.9
III. Institute of Forest Genetics										
Interpopulation crosses:										
Blue	Green	8	8	118	86.4	8.6	(0.9)	4.7	(0.6)	50.1
Blue	F ₁	2	2	15	100.0	50.8	(1.8)	41.2	(6.0)	86.9
F ₁ ³	Blue	2	1	4	100.0	8.5	—	2.5	—	14.7
F ₁	Green	2	1	7	71.4	45.6	—	3.0	—	6.6
F ₁	F ₁	5	3	19	78.9	18.3	(3.0)	2.2	(0.6)	9.5
Within-population crosses:										
Blue	Blue	10	10	178	44.9	6.7	(0.6)	4.0	(0.5)	67.2

RESULTS

Crosses of northern Pinus muricata populations. Crossability between blue and green trees from all northern sources averaged 100% (Table 3). In crosses on native trees, the average number of sound seeds from blue \times green crosses was significantly higher than the blue \times blue control crosses. Germination percents of green \times blue and blue \times green crosses did not differ significantly from the blue \times blue control crosses. In crosses at Russell Reservation, the average numbers of sound seeds and germination percents from green \times blue crosses did not differ significantly from the green \times green control crosses. The lower seed set for the blue control crosses at Russell was probably due to premature opening of the unbagged cones, which permitted some seed to shed before harvesting. The percent germination of these crosses was only slightly lower than the other control and blue \times green families. Blue \times green crosses on trees at IFG produced numbers of sound seed similar to those in blue \times blue control crosses.

Crosses on F_1 females produced fewer sound seeds than either the within-population crosses or crosses that used the F_1 as male (Table 3). At IFG, the average numbers of viable seeds and percent germination for crosses involving the F_1 females were significantly lower than results from the blue \times blue cross. At Russell, however, results from backcrosses using the F_1 's as males did not differ significantly from the blue \times blue and green \times green crosses.

Viable seed from all blue \times green crosses and crosses involving the F_1 's were sown in a nursery. Heights of seedlings from all crosses did not differ significantly through their second year. The only differences in survival were between crosses on F_1 females (\bar{x} = 33%) and all other crosses (\bar{x} > 80%).

Crosses of widespread Pinus muricata populations. Crossability generally decreased with increased distance between populations (Table 4). The blue populations north of Sea Ranch crossed easily with the Marin population (crossability > 100%); easily with the Monterey population in one direction (using a blue female, > 100%), but less easily in the reciprocal cross (52%); and did not cross at all with green trees from Purisima or San Vicente (0%).

The green population in southern Sonoma Co. crossed less readily than the blue population with Monterey trees (crossability = 27%) and was nearly unsuccessful (< 5%) in crosses with San Vicente trees. Marin trees followed a similar pattern: low success with Monterey (26%) and no seed from a single attempt with Santa Cruz Island (0%). Crossability between Monterey and Purisima was very low (6%).

Populations south of Monterey were highly interfertile. Crossability of the San Vicente \times Purisima combination was 82%, and

TABLE 4. SUMMARY OF CROSSES AT THE INSTITUTE OF FOREST GENETICS AMONG WIDESPREAD CLOSED CONE PINE POPULATIONS. ¹CI = 95% confidence interval, based on average results per attempt, not per cone. ²Expressed as average percent of total number of seeds/cone that germinated. ³Each female pollinated with a mix of the same 2 males.

Parents		At-tempts	At-tempts producing sound seeds	Female strobili pollinated	Percent of strobili producing cones	Total number of seeds/cone		Number of viable seeds/cone		Germinable seed (%) ²
Females	Males					Mean	CI ¹	Mean	CI ¹	
I. Interpopulation crosses										
Mendocino Co.	Marin Co.	2	2	39	56.4	12.2	(1.5)	4.9	(1.1)	42.2
	Monterey	2	2	29	86.2	21.0	(1.4)	8.5	(0.1)	40.4
	Purisima	2	0	30	83.3	17.4	(0.8)	0.0	—	—
Monterey	Mendo./Son. Cos.-Blue	4	4	97	33.0	7.4	(3.3)	4.7	(2.3)	68.6
	Son. Co.-Green	4	3	74	28.4	5.2	(2.7)	2.4	(0.7)	72.6
	Marin Co.	2	2	58	74.1	6.0	(0.7)	2.3	(0.4)	38.2
	Purisima	2	2	41	60.9	5.8	(1.3)	0.5	(<0.1)	8.1
Sta. Cruz I.	Marin	1	1	7	42.8	9.3	—	0.0	—	—
	Santa Rosa Island	1	1	6	16.7	15.0	—	14.0	—	93.3
San Vicente	Mendocino	2	0	24	75.0	3.3	(1.4)	0.0	—	—
	Son. Co.-Green	2	1	35	45.7	0.8	(0.2)	0.1	—	10.0
	Purisima	2	2	25	72.0	11.5	(7.2)	1.8	(1.1)	15.5
	Guadalupe Island	1	0	10	10.0	4.0	—	0.0	—	—
	Cedros Island	1	0	19	36.8	5.0	—	0.0	—	—
II. Within-population crosses										
Mendocino Co.	Mendo./Son. Cos.-Blue	10	10	178	44.9	6.7	(0.6)	4.0	(0.5)	67.2
Monterey	Monterey	1	1	32	46.8	10.0	—	9.0	—	90.0
San Vicente	San Vicente	3 ³	3 ³	27	81.5	11.0	(5.2)	2.2	(1.1)	22.0

although the control cross was lacking, the Santa Cruz \times Santa Rosa combination set more seed on average than any of the controls. In two attempts to cross San Vicente *P. muricata* with Guadalupe and Cedros Island pines, none of the 39 seeds produced was viable (0%).

First-year nursery heights and survival did not differ significantly between seedlings from interpopulational crosses and control crosses.

DISCUSSION

Crossability of Pinus muricata. Crossing data support conclusions from previous studies of growth, form, and anatomical traits that *P. muricata* is a highly polymorphic species, with great intra- and interpopulation variability, especially in the southern mainland and island populations. Relationships among the populations of Californian closed-cone pines are illustrated in a crossing polygon (Fig. 2). We redefined three distinct breeding units (Critchfield 1967) within *P. muricata*: 1) northern *P. muricata* populations from Marin Co. northward; 2) southern *P. muricata* populations including mainland and Channel Islands populations from Purisima southward; and 3) Monterey *P. muricata*, which remains intermediate between the first two units. *Pinus radiata*, including Guadalupe and Cedros Island pines, and *P. attenuata* remain distinct from northern and central bishop pine, but appear weakly related to certain southern *P. muricata* populations.

The occurrence of barriers to hybridization among widespread *P. muricata* populations led Critchfield (1967) to hypothesize that the genetic differences between blue and green races in northern California also are maintained by crossing barriers. Contrary to this speculation, we found no post-pollination barriers in crosses between contiguous blue (Mendocino and northern Sonoma cos.) and northern green (central Sonoma Co.) populations. These results corroborate prior indications of natural hybridization in Sonoma Co. from terpene (Mirov et al. 1966) and isozyme evidence (Millar 1983). Natural introgression may be inhibited, however, by differences in flowering times and by lower fertility in the hybrid female strobili.

In the limited number of combinations we made, the Marin and Monterey *P. muricata* populations responded more like northern *P. muricata* than the southern populations of the species. Monterey (green) trees set only a few viable seeds in combination with Santa Cruz Island pines, but had moderate crossability in combinations with Marin and Sonoma-green populations and moderate to high crossability to Sonoma/Mendocino blue populations. The southern breeding unit defined by Critchfield now can be expanded to include Purisima.

Phylogenetic inferences. Patterns of crossability supplement previous studies of phylogenetic relationships in *P. muricata*. The ex-

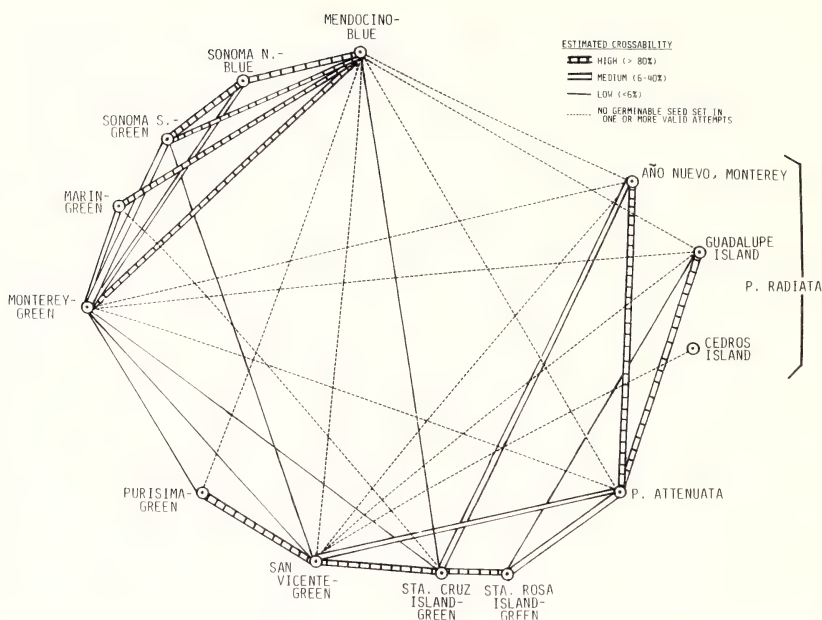


FIG. 2. Crossing relationships in the California closed-cone pines, including all available information to date. All populations not labeled with a species name are *P. muricata*.

istence and maintenance of abrupt genetic discontinuities in morphological and biochemical traits between blue and green races of *P. muricata* at Sea Ranch in northern California are difficult to interpret. Forests of *P. muricata* are continuous through a narrow (2 km) transition, and no environmental or ecological changes coincide with the discontinuity. Our crossing studies showed that the races have remained interfertile. This suggests that, despite genetic differences in several traits, the Sonoma green population and northern Mendocino populations are closely related. The races appear to have evolved recently in a mosaic pattern that did not affect interpopulation fertility except possibly at the F_2 level. Although blue and green populations can hybridize, other barriers, such as differences in phenology (Millar 1983) and different responses to soils (Millar unpubl. data), may contribute to keeping the contiguous races distinct.

Duffield's (1951) proposal that a distinct northern race of *P. muricata* exists is re-enforced by reproductive barriers between northern and southern groups. From an analysis of many traits, Duffield concluded that populations in Humboldt, Mendocino, and Sonoma cos. are a distinct variety and that Marin and Monterey are intermediate between this northern variety and the rest of the species. Axelrod

(1983) formally published the northern variety as *P. muricata* var. *borealis*. He based the description, however, only on cone shape and extended var. *borealis* south to include some "relict trees" at Monterey. Axelrod's designation leaves *P. muricata* var. *borealis* unsatisfactorily heterogeneous in other traits (Table 1), and suggests that two sympatric varieties somehow maintain their genetic integrity at Monterey. Crossing relationships show Marin and Monterey populations to be distinct and intermediate, although they have greater affinities to northern than to southern populations. We suggest that the varietal designation conservatively be limited to populations north of Marin Co.

The infertility between the northern populations of *P. muricata* (e.g., Mendocino) and *P. radiata* and *P. attenuata* suggests that var. *borealis* has diverged considerably from common ancestors of the Californian closed-cone pines, and from closely related species. In contrast, the southern populations of *P. muricata*, especially the San Vicente and Channel Islands populations, are sufficiently similar to allow successful interspecific hybridization. Apparently evolution in these taxa has not affected hybridization potential.

Evolutionary interpretations of central and southern *P. muricata* populations (summarized in Millar 1986) have also differed depending on the emphasis given cone morphology. Mason (1930, 1949) and Axelrod (1967, 1980, 1983) argue that pines having symmetric cones with smooth apophyses represent an independent evolutionary lineage (*P. remorata* Mason). Mason restricts this designation to pines with symmetric cones on the Channel Islands, whereas Axelrod uses the name for all trees with this cone type wherever they occur on the islands and mainland. Both authors suggest that the present variation in cone traits, typical of many stands south of Sonoma Co., resulted from hybridization of *P. remorata* with *P. muricata*. Other authors have concluded that cone shape is just one of many variable traits in *P. muricata* (Duffield 1951, Fielding 1961, Linhart et al. 1967, Doran 1974). In quantitative analyses, Linhart et al. (1967) found that distinct variation in resin canals, terpenes, and several needle anatomy traits did not correlate with cone variation, and concluded that *P. remorata* was "primarily a name given a particular cone type in a variable species".

We found no support from crossing studies for the hypothesis that *P. remorata* is a distinct taxon from *P. muricata*. Although most of our breeding trees were not identified individually by cone type, all our pollen and seed lots from Marin south contained trees with the smooth, symmetric cone type. Pines sampled from the Channel Islands, especially those from Santa Rosa, had high frequencies of smooth cones. We found no pattern of crossability to suggest that these trees were distinct taxonomically. The Channel Islands pines resembled southern populations of *P. muricata* in crossing behavior

among all populations tested. Furthermore, if *P. remorata* extends north to Monterey and Marin (Axelrod 1980), we would expect to find greater crossability between those populations and Channel Islands populations than was found. Observations on resin canals indicated that number of canals varied greatly among trees, and that variation was related to geographical location and not to cone type. Thus, we found no evidence that smooth, symmetric cones found on trees throughout the species are indicators of an independent lineage.

CONCLUSIONS

Crossing results reported here supplemented and corroborated other studies on *P. muricata* which indicate that complex patterns of variation exist in the species. Unique in *Pinus* is the presence of intraspecific post-pollination barriers among *P. muricata* populations. These barriers, together with distinguishing patterns of variation in other traits, suggest that the northern and southern populations have long been isolated and perhaps should be considered distinct species. By contrast, evolution of genetic differences between blue and green races within the northern populations has not been accompanied by evolution of post-reproductive barriers. Genetic differences between these races must be maintained by other factors.

Since southern *P. muricata* populations retain crossability to *P. radiata* and *P. attenuata*, the great variation in these populations may have been imported through prior interspecific hybridization. Patterns of crossability, coupled with evidence from variation in other traits, gave no evidence to suggest that the smooth, symmetric cone type alone is an indicator of a distinct evolutionary lineage within the species complex. This cone type is found in nearly all *P. muricata* populations and appears to be one of many polymorphic traits in the species.

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ENDEMIC VASCULAR PLANTS OF NORTHWESTERN CALIFORNIA AND SOUTHWESTERN OREGON

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ABSTRACT

An account of the endemic vascular plants of northwestern California and southwestern Oregon is presented. This component of the California Floristic Province, known for its high species richness, was found to have a large number of neoendemics in a regional flora generally characterized as relictual in nature. A list of endemics provides distribution by county and formal designations of rarity and endangerment for 281 taxa in 42 families.

The flora of northwestern California and southwestern Oregon has long been known for its high floristic richness (Stebbins and Major 1965). We estimate that there are over 3500 taxa of vascular plants, in about 150 families and 760 genera, in northwestern California alone (Smith and Sawyer 1987). The region may be viewed as the last major frontier along the Pacific Coast to be studied in detail. Intensive collecting began only about 20 years ago, after the pioneering work of Alice Eastwood, Joseph P. Tracy, Thomas Jefferson Howell, Edward Greene, Milo Baker, and Doris Niles. Our work in the last two decades, along with our students and colleagues (Muth 1967, Ferlatte 1974, Oettinger 1975, Barker 1979, Nelson 1979, Stillman 1980, Whipple 1981), has resulted in a more detailed knowledge of this interesting flora. Recent efforts at determining the status of rare and endangered plants in both states also has added greatly to our knowledge (Siddall et al. 1979, Meinke 1981, Smith and York 1984, Soper et al. 1985, York 1985). We now have a good account of the endemic vascular flora of this region.

STUDY AREA

Northwestern California and southwestern Oregon, a region of about 55,000 km², are considered part of the California Floristic Province (Howell 1955, 1956, 1957, Noldenke and Howell 1960, Stebbins and Major 1965, Raven and Axelrod 1978). Therefore, for both floristic and geographic reasons, the plants endemic to southwestern Oregon also are included here. Whereas the Klamath Mountains and the North Coast Ranges represent only 15% of the area of the California Floristic Province, they include some 65% of the 4452 native taxa found growing in the province as a whole (Raven and Axelrod 1978). The floristic diversity here is exceptional.

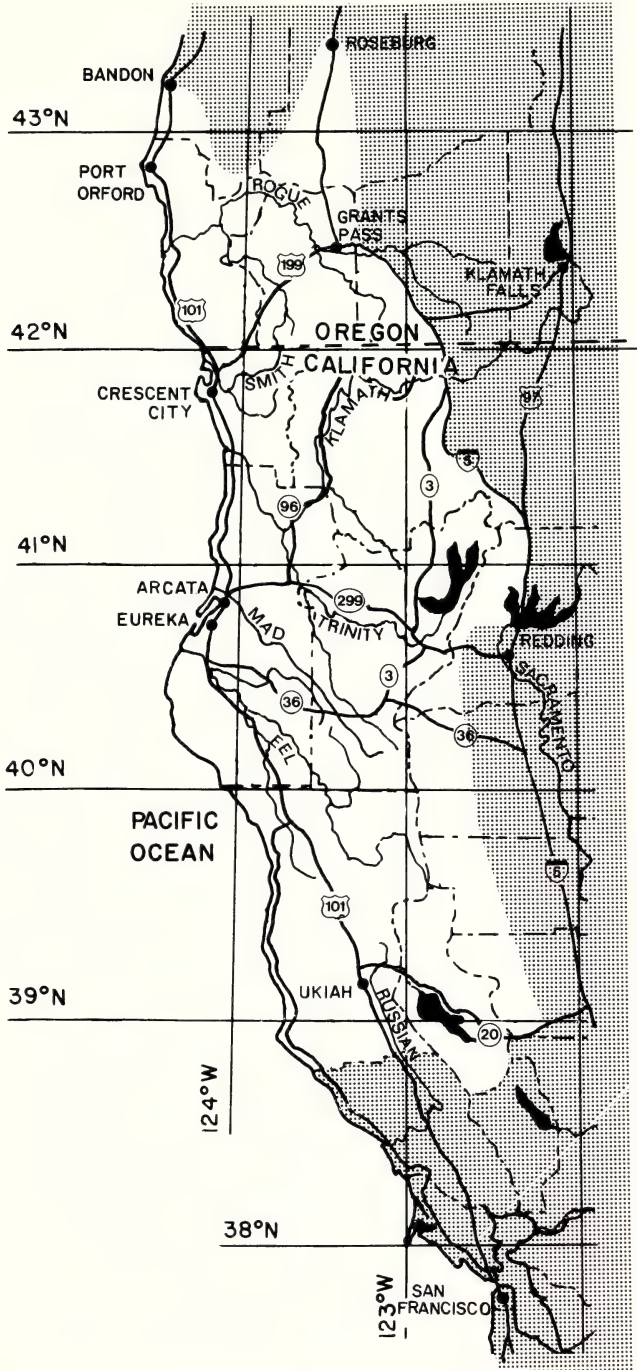


FIG. 1. Location of the study area in northwestern California and southwestern Oregon (shown in white).

The study area (Fig. 1) centers on the Klamath Mountains, a geologic province of ancient rocks and landforms (Irwin 1960, 1981). They constitute a poorly defined set of ranges, including the Eddies, Marbles, Salmons, Scott Bars, Scotts, Siskiyou, Trinities, Trinity Alps, and the Yolla Bollys. We also include the topographically continuous North Coast Ranges of California to the west and to the south of the Klamath Mountains. Lake and Mendocino cos. mark the southern extent of the region; counties farther south lack the montane environments present to Snow Mountain (Heckard and Hickman 1984). Northwestern California is treated by a checklist of the vascular plants (Smith and Sawyer 1987) and by a key to families and genera (Smith and Sawyer 1981).

The traditional explanation for the area's rich flora is that it is a mixture of California and northern plants. It is not surprising that plants from the north and from the south occur here. The area is geographically and environmentally central on the West Coast of North America (Whittaker 1961), and geologically complicated, with its many disjunct areas of ultramafic rock (Whittaker 1960, Sawyer and Thornburgh 1977, Kruckeberg 1984). In addition, the ancient terrain supports great habitat variety in a moderated, maritime climate (Richerson and Lum 1980). The area, especially the Klamath Mountains, is viewed as a refugium of Tertiary plants (Wolfe 1969, Axelrod 1976).

TYPES OF ENDEMISM

The relictual nature of the flora is seen in many families and genera, although not all of them appear in the list of endemic taxa because they also occur outside of the region. *Aruncus dioicus*, *Calypso bulbosa*, *Darlingtonia californica*, *Disporum hookeri*, *Euonymus occidentalis*, *Mahonia nervosa*, *Polystichum munitum*, *Sequoia sempervirens*, and *Trautvetteria carolinensis* are typical of the many "Arcto-Tertiary" plants that grow in the Klamath Mountains or along the coast at lower elevations.

In addition, the flora is seen as being enriched by plants of Mexican origin, such as *Arbutus*, *Garrya*, and *Gaultheria* that now grow with *Sequoia* in the redwood forest (Abrams 1925, Axelrod 1977). Many of these southern elements grow in the woodlands, chaparral, and grasslands found at lower elevations or near the coast. The events of the Pleistocene and hypsithermal are also seen as causing further accumulations of various plants from the north, such as *Empetrum nigrum* and *Menyanthes trifoliata*; of *Purshia tridentata* and *Forsselia stipulifera* from the Great Basin; and of *Pinus sabiniana* from central California.

The relictual nature of the flora can also be evaluated by a review of a list of endemics (Appendix 1). Plants without close relatives or

those whose close relatives are disjunct are typically considered paleoendemic or relicts (Stebbins 1980). *Kalmiopsis leachiana*, *Picea breweriana*, *Quercus sadleriana* (Tucker 1983), and *Cornus sessilis* are good examples. But the list contains surprisingly few relicts.

In this geologically stable area, with its moderated climate, we might also expect to find a larger number of endemic species, and perhaps even endemic genera (Kruckeberg and Rabinowitz 1985). Only two monotypic genera, *Bensoniella* and *Tracyina*, are endemic. Others, such as *Cycladenia humilis*, *Darlingtonia californica*, and *Whitneya dealbata*, often thought to be endemic to the region, are not.

To summarize, the centrally positioned, continuous montane environment among the North Coast Ranges, the Klamath Mountains, the Cascades, and the Sierra Nevada accounts for much of the floristic richness, but not for the degree of endemism. Similarly, the invoking of paleoendemism, taken by itself, is not adequate.

ANALYSIS OF THE ENDEMIC FLORA

In surveying the list of endemic taxa, we were impressed by the large number of infraspecific taxa. In this observation lies another explanation for the local level of endemism. Some of the taxa, such as *Iris tenax* subsp. *klamathensis*, *Dicentra formosa* subsp. *oregana*, and *Holodiscus discolor* var. *delnortensis*, represent regional variants of widespread, western species. Others, such as *Juniperus communis* var. *jackii* and *Chlorogalum pomeridianum* var. *minus*, are typical of serpentine substrates. Some plants, as in *Trillium ovatum* subsp. *oettingeri*, grow at higher elevations than do the typical forms of the species. Still others, such as *Monardella odoratissima* subsp. *pallida* and *Penstemon newberryi* subsp. *berryi*, appear to be local expressions of common Sierran species.

To evaluate further the list of endemics, genera with five or more taxa were singled out and appear in Table 1. Many of them, such as *Arabis*, *Penstemon*, or *Lupinus*, are expected, as they are known for their diversity in the western United States. Other large genera, such as *Aster*, *Carex*, *Lotus*, or *Phlox*, are conspicuously absent.

The number of endemic species can be compared to the total taxa in each genus. For example, *Phacelia* is a genus of about 200 species, of which 29 grow in the area, seven of them endemic. A few genera, such as *Arabis*, *Horkelia*, *Lilium*, and *Limnanthes*, stand out as being unusually high in regional endemics. Of all of the taxa tallied, *Lewisia*, *Sedum*, and *Sidalcea* have an exceptionally high number of regional endemics.

Such comparisons might be better judged in a larger geographical context. Table 1 also shows the number of taxa for California (Munz 1959, 1968). A larger number of species and infraspecific taxa would

TABLE 1. GENERA IN NORTHWESTERN CALIFORNIA AND SOUTHWESTERN OREGON WITH FIVE OR MORE ENDEMIC TAXA. The fraction represents the number of species/number of subspecific taxa. Estimates for size in each genus are after Willis (1973); those with "*" are from Raven and Axelrod (1978). Taxa in the region itself are from Peck (1961), Smith and Sawyer (1987), and recent monographs. The values in parentheses are species : taxa ratios. If all taxa are at the species rank, the ratio equals 1.0.

Genus	No. species per genus	Endemics in area	Taxa in area	Taxa in California
I. Large genera, <100 species				
<i>Arabis</i>	120	7/8 (1.1)	21/26 (1.2)	35/52 (1.5)
<i>Epilobium</i>	215	6/6 (1.0)	18/22 (1.2)	36/22 (1.6)
<i>Eriogonum</i>	250	10/11 (1.1)	33/47 (1.4)	104/158 (1.5)
<i>Lupinus</i>	200*	8/9 (1.1)	36/54 (1.5)	82/144 (1.8)
<i>Penstemon</i>	250*	5/5 (1.0)	20/27 (1.4)	49/75 (1.2)
<i>Phacelia</i>	200	7/7 (1.0)	29/31 (1.1)	91/116 (1.3)
<i>Plagiobothrys</i>	100	4/5 (1.2)	17/20 (1.1)	39/50 (1.3)
<i>Sedum</i>	600	5/10 (2.0)	11/20 (1.8)	12/18 (1.5)
II. Moderate-sized genera, 10–80 species				
<i>Arctostaphylos</i>	50*	7/7 (1.0)	16/21 (1.3)	32/53 (1.7)
<i>Calochortus</i>	60	6/6 (1.0)	16/18 (1.1)	39/52 (1.3)
<i>Horkelia</i>	30	4/5 (1.2)	8/10 (1.2)	16/25 (1.6)
<i>Lewisia</i>	20	3/6 (2.0)	8/11 (1.4)	13/18 (1.4)
<i>Lilium</i>	80	5/5 (1.0)	11/12 (1.1)	15/19 (1.3)
<i>Limnanthes</i>	10*	3/5 (1.7)	4/9 (2.3)	7/11 (1.6)
<i>Sidalcea</i>	25	3/7 (2.3)	9/21 (2.3)	18/33 (1.8)

be expected for this larger area. One way to reduce the effect of area is to express the numbers as ratios. *Lupinus*, for example, is a genus of about 200 species. Munz reports 82 species and 144 subspecies and varieties in California. There are, then, almost two infraspecific taxa per species of *Lupinus* in the state.

When northwest California is compared to the state as a whole, a predicted pattern is seen, i.e., the smaller the area, the smaller the ratio. California includes those taxa of the Sierra Nevada, the Cascades, the Klamaths, and the North Coast in the tally, so that the ratio would be larger than that for the northwest section of the state alone. Furthermore, the ratio for endemics would be expected to be even smaller yet, because they are restricted to a smaller area. The expected ratio reduction does occur for most of the genera in Table 1. Exceptions are *Lewisia*, *Sedum*, and *Sidalcea*, where the ratio increases. This is taken as evidence that adaptive radiation is occurring in the region. We conclude, therefore, that northwest California and southwest Oregon is not only a refugium, but it is also an area of active diversification today.

An abundance of local varieties and subspecies is expected as populations adapt to the unique set of environmental controls

(Kruckeberg and Rabinowitz 1985). The region's heterogeneity of topography and parent material offers the setting for this diversification. Stebbins and Major (1965), using Lake Co., California, an area containing volcanic, sedimentary, and ultramafic substrates, argued that under such settings neoendemics would be developed during periods of changing climate. Axelrod (1982) makes a similar argument for the Monterey endemic area. The celebrated patchy matrix of habitats found in northwest California and southwest Oregon supplies a larger stage for the addition of a high number of new taxa into the region's flora during the recent period of climatic change.

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APPENDIX 1. ANNOTATED CATALOGUE OF ENDEMIC VASCULAR PLANTS

County abbreviations: CALIFORNIA. COL = Colusa; DNT = Del Norte; GLE = Glenn; HUM = Humboldt; LAK = Lake; MEN = Mendocino; SHA = Shasta; SIS = Siskiyou; TEH = Tehama; TRI = Trinity. OREGON. COS = Coos; CUR = Curry; DOU = Douglas; JAC = Jackson; JOS = Josephine.

A-1 to A-4 indicates that the plant is listed in Smith and York (1984).

- A-1 = Plants of highest priority
- A-2 = Plants rare or endangered in California, but more common elsewhere
- A-3 = Plants about which we need more information
- A-4 = Plants of limited distribution

B-1 to B-3 indicates that the plant is listed in Siddall et al. (1979).

- B-1a = Very local endemic
- B-1b = Regional endemic
- B-2a = Plants thinly scattered over a wide range
- B-2b = Known only from a few widely disjunct populations
- B-3 = Of concern in Oregon, more abundant elsewhere

C indicates that the plant is listed in Meinke (1981).

D-1 to D-3 indicates that the plant is listed in Soper et al. (1985).

- D-1 = Taxa endangered or threatened throughout range, including those possibly extinct
- D-2 = Taxa endangered or threatened in Oregon, but more common or stable elsewhere
- D-3 = Taxa limited in abundance throughout range, but currently stable

PINOPHYTA

Cupressaceae

Juniperus communis Linnaeus var. *jackii* Rehder. DNT, SIS; CUR.

Pinaceae

Picea breweriana Watson. DNT, HUM, TRI, SIS; COS, CUR, JAC, JOS.

MAGNOLIOPHYTA: MAGNOLIOPSIDA

Berberidaceae

Mahonia nervosa (Pursh) Nuttall var. *mendocinensis* (Roof) Roof. MEN; A-3.
Vancouveria chrysantha Greene. DNT, SIS; CUR, JOS; A-4, B-1b.

Boraginaceae

Cryptantha clevelandii Greene var. *dissita* (I. M. Johnston) Jepson & Hoover. LAK.
Cryptantha crinita Greene. SHA, TEH; A-1.
Hackelia amethystina J. T. Howell. GLE, LAK, MEN, TEH, TRI; A-4.
Hackelia bella (Macbride) I. M. Johnston. HUM, MEN, SIS, TEH, TRI.
Plagiobothrys hirtus (Greene) I. M. Johnston var. *corallicarpa* (Piper) I. M. Johnston.
 JAC, JOS; B-1b, C, D-1.
Plagiobothrys hirtus (Greene) I. M. Johnston var. *hirtus*. DOU; B-1b, C.
Plagiobothrys lamprocarpus (Piper) I. M. Johnston. JOS; B-1a, C, D-1.
Plagiobothrys lithocaryus (Greene ex A. Gray) I. M. Johnston. LAK, MEN; A-4.
Plagiobothrys tener (Greene) I. M. Johnston var. *subglaber* I. M. Johnston. LAK.

Campanulaceae

Campanula shetleri Heckard. SHA, SIS; A-1.

Caryophyllaceae

- Minuartia decumbens* T. W. & J. P. Nelson. SHA, TEH, TRI; A-1.
Minuartia howellii (Watson) Mattfeld. DNT; CUR, JOS; A-4.
Minuartia nuttallii (Pax) Briquet subsp. *gregaria* (Heller) Maguire. COL, HUM, LAK, MEN, SIS, TEH, TRI; CUR, JAC, JOS.
Minuartia rosei (Maguire & Barneby) McNeill. SHA, TEH, TRI; A-4.
Silene campanulata Watson subsp. *campanulata*. MEN; A-1.
Silene hookeri Nuttall ex Torrey & A. Gray subsp. *bolanderi* (A. Gray) Abrams. HUM, MEN, TRI; CUR, JOS; B-3, D-2.
Silene hookeri Nuttall ex Torrey & A. Gray subsp. *pulverulenta* (Peck) Hitchcock & Maguire. JAC, JOS; B-1b.
Silene marmorensis Kruckeberg. SIS; A-1.

Compositae

- Antennaria suffrutescens* Greene. DNT, HUM; CUR, JOS; A-4.
Arnica cernua T. J. Howell. DNT, HUM, SIS, SHA, TRI; COS, CUR, JOS; A-4.
Arnica spathulata Greene subsp. *eastwoodiae* (Rydberg) Ediger & Barkley. DNT, HUM, SIS; CUR, DOU, JAC, JOS; A-4.
Arnica venosa Hall. SHA, TRI; A-4.
Aster brickellioides Greene var. *brickellioides*. DNT, SIS; CUR, JAC, JOS; A-4.
Aster siskiyouense Nelson & Macbride. GLE, SIS, TEH, TRI; JAC, JOS.
Balsamorhiza sericea Weber. TRI, SIS; JOS; A-4, B-1b, C, D-1.
Chaenactis suffrutescens A. Gray. SIS, TRI; A-4.
Cirsium acanthodontum Blake. DNT, HUM; COS, CUR, DOU.
Cirsium ciliolatum (Henderson) J. T. Howell. SIS; JAC; A-1, B-1b, D-3.
Erigeron bloomeri A. Gray var. *nudatus* (A. Gray) Cronquist. DNT, SIS; JAC, JOS; A-2.
Erigeron bloomeri A. Gray var. *pubens* Keck. SIS, TEH, TRI.
Erigeron delicatus Cronquist. DNT; CUR, JOS; A-3, B-1b, C.
Erigeron flexuosus Cronquist. DNT, SHA, TRI; A-1.
Eriophyllum lanatum (Pursh) Forbes var. *aphanactis* J. T. Howell. GLE, COL, LAK.
Eriophyllum lanatum var. *lanceolatum* (T. J. Howell) Jepson. DNT, HUM, SIS, TEH, TRI; CUR, JAC, JOS.
Eupatorium shastense Taylor & Stebbins. SHA; A-4.
Grindelia stricta De Candolle subsp. *blakei* (Steyermark) Keck. HUM; A-1.
Haplopappus ophitidis (J. T. Howell) Keck. SHA, TEH, TRI; A-4.
Haplopappus racemosus (Nuttall) Torrey subsp. *congestus* (Greene) Hall. DNT; CUR, DOU, JAC, JOS; A-4, C.
Haplopappus racemosus subsp. *pinetorum* Keck. SIS, TRI.
Hazardia whitneyi (A. Gray) Greene var. *discoideus* (J. T. Howell) D. Clark. GLE, HUM, LAK, SIS, TRI; DOU, JOS; B-3, D-2.
Helianthella californica A. Gray var. *shastensis* W. Weber. SHA, SIS, TRI.
Hemizonia calyculata (Babcock & Hall) Keck. LAK, MEN; A-4.
Hemizonia tracyi (Babcock & Hall) Keck. HUM, MEN, TRI; A-4.
Heterotheca breweri (A. Gray) Shinnars var. *multibracteata* Jepson. SIS, TEH, TRI.
Lasthenia macrantha (A. Gray) Greene subsp. *prisca* Ornduff. CUR; B-1b, C, D-3.
Madia doris-nilesiae T. W. Nelson & J. P. Nelson. TRI.
Madia gracilis (Small) Keck subsp. *pilosa* Keck. HUM.
Madia stebbinsii T. W. & J. P. Nelson. TEH, TRI; A-1.
Microseris detlingii Chambers. JAC; B-1a, C.
Microseris howellii A. Gray. DNT; CUR, JAC, JOS; B-1b, C, D-1.
Microseris laciniata (Hooker) Schulz-Bipontinus subsp. *siskiyouensis* Chambers. DNT, HUM, SIS; CUR, JOS.
Raillardella pringlei Greene. SIS, TRI; A-1.
Rudbeckia californica A. Gray var. *glauca* Blake. DNT, TRI; CUR, DOU, JOS.

Rudbeckia californica A. Gray var. *intermedia* Perdue. SIS, TRI.
Senecio greenei A. Gray. GLE, LAK, MEN, TRI.
Senecio hesperius Greene. CUR, JOS; B-1b, C, D-1.
Tracyina rostrata Blake. HUM, LAK; A-1.
Wyethia longicaulis A. Gray. HUM, MEN, TRI; A-4.

Convolvulaceae

Calystegia collina (Greene) Brummitt subsp. *tridactylosa* (Eastwood) Brummitt. MEN.

Crassulaceae

Parvisedum leiocarpum (H. K. Sharsmith) Clausen. LAK; A-1.
Sedum laxum (Britton) Berger subsp. *eastwoodiae* (Britton) Clausen. MEN; A-1.
Sedum laxum (Britton) Berger subsp. *flavidum* Denton. DNT, HUM, SIS, TRI; A-1.
Sedum laxum (Britton) Berger subsp. *heckneri* (Peck) Clausen. DNT, HUM, SIS, TRI; CUR, JAC, JOS; A-4, D-3.
Sedum laxum (Britton) Berger subsp. *latifolium* Clausen. DNT.
Sedum laxum (Britton) Berger subsp. *laxum*. DNT, SIS; CUR, JAC, JOS.
Sedum moranii Clausen. JOS; C, D-1.
Sedum oblanceolatum Clausen. SIS; JAC; C.
Sedum obtusatum A. Gray subsp. *paradisum* Denton. SHA, TRI; A-1.
Sedum obtusatum A. Gray subsp. *retusum* (Rose) Clausen. LAK, MEN, SIS, TRI; CUR, JAC.
Sedum radiatum Watson subsp. *depauperatum* Clausen. SIS; JOS; A-3.

Cruciferae

Arabis aculeolata Greene. DNT, SIS; CUR, JOS; A-1, C.
Arabis koehleri T. J. Howell var. *koehleri*. DOU, JOS; B-1b, C, D-1.
Arabis koehleri T. J. Howell var. *stipitata* Rollins. CUR, JOS; C, D-3.
Arabis macdonaldiana Eastwood. DNT, MEN; CUR, JOS; A-2, C, D-1.
Arabis oregona Rollins. MEN, SIS, TRI; JAC, JOS; A-3.
Arabis rigidissima Rollins. HUM, SIS, TRI; A-4.
Arabis serpentinicola Rollins. SIS; CUR; A-1, B-1b, C.
Arabis subpinnatifida Watson. GLE, HUM, MEN, SIS; DOU, JAC, JOS.
Cardamine gemmata Greene. DNT, SIS; CUR, JAC, JOS; A-1, B-1b, D-2.
Draba carnosula O. E. Schulz. SIS, TRI; A-1.
Draba howellii Watson. DNT, HUM, SHA, SIS, TRI; JOS; A-4, B-1b, D-1.
Draba pterosperma Payson. SIS; A-4.
Streptanthus barbatus Watson. SIS, TEH, TRI.
Streptanthus howellii Watson. DNT; CUR, JOS; A-2, B-1b, C, D-1.
Streptanthus tortuosus Keller var. *pallidus* Jepson. HUM, SIS, TRI.
Thlaspi montanum Linnaeus var. *californicum* (Watson) P. Holmgren. HUM; A-1.
Thlaspi montanum Linnaeus var. *siskiyouense* P. Holmgren. CUR, JOS; C, D-3.

Cuscutaceae

Cuscuta salina Engelmann var. *papillata* Yuncken. MEN.

Ericaceae

Arctostaphylos × *cinerea* T. J. Howell. DNT; CUR, DOU, JOS.
Arctostaphylos hispidula T. J. Howell. DNT, HUM; CUR, JOS; A-4, B-1b, C, D-3.
Arctostaphylos klamathensis Edwards, Keeler-Wolf, & Knight. SIS; A-1.
Arctostaphylos knightii Gankin & Hildreth. DNT, HUM.
Arctostaphylos manzanita Parry subsp. *roofii* (Gankin) P. V. Wells. LAK, TEH.

- Arctostaphylos stanfordiana* Parry subsp. *raichei* Knight. LAK, MEN.
Arctostaphylos tracyi Eastwood. DNT, HUM, MEN.
Kalmiopsis leachiana (Henderson) Rehder. CUR, DOU, JOS; C.
Rhododendron occidentale (Torrey & A. Gray) var. *paludosum* Jepson. HUM, DNT.

Euphorbiaceae

- Chamaesyce ocellata* (Durand & Hilgard) Millsbaugh var. *rattanii* (Watson) Koutnik.
GLE, TEH; A-4.

Fagaceae

- Quercus garryana* Douglas var. *breweri* (Engelmann in Watson) Jepson. LAK, HUM,
MEN, SIS, TRI; CUR, JAC, JOS.
Quercus sadleriana R. Brown of Campster. DNT, SIS, TEH; COS, CUR, DOU, JAC,
JOS.

Fumariaceae

- Dicentra formosa* (Haworth) Walpers subsp. *oregana* (Eastwood) Munz. DNT, HUM,
SIS, TRI; CUR, JOS; A-4, B-1b, C.

Garryaceae

- Garrya buxifolia* A. Gray. DNT, HUM, MEN, SIS; CUR, JOS.

Gentianaceae

- Gentiana bisetacea* T. J. Howell. CUR, JOS; C, D-1.
Gentiana setigera A. Gray. HUM, MEN, SIS, TRI; JAC, JOS; A-3.

Grossulariaceae

- Ribes inerme* Rydberg var. *subarmatum* Peck. JAC.
Ribes marshallii Greene. HUM, SIS; JAC, JOS; A-4, B-3, D-2.

Hydrophyllaceae

- Phacelia argentea* Nelson & Macbride. DNT; COS, CUR; A-1, B-1b, C, D-1.
Phacelia capitata Kruckeberg. COS, DOU, JAC; B-1b, C.
Phacelia cookei Constance & Heckard. SIS; A-1.
Phacelia dalesiana J. T. Howell. SIS, TRI; A-1.
Phacelia greenei J. T. Howell. SIS, TRI; A-1.
Phacelia leonis J. T. Howell. SIS, TRI; JOS; A-3, B-1b, D-2.
Phacelia pringlei A. Gray. SIS, TRI; JAC; A-1.

Labiateae

- Monardella purpurea* T. J. Howell. DNT, HUM, SIS; CUR, JOS; A-4, B-1b, D-2.
Stachys rigida Nuttall ex Bentham subsp. *lanata* Epling. DNT, HUM.

Leguminosae

- Astragalus agnicidus* Barneby. HUM; A-1.
Astragalus rattanii A. Gray var. *rattanii*. COL, HUM, MEN, LAK, TRI.
Lathyrus biflorus T. W. Nelson & J. P. Nelson. HUM; A-1.
Lathyrus delnorticus C. L. Hitchcock. DNT; COS, CUR, JOS; A-4, B-1b, D-2.
Lathyrus glandulosus Broich. HUM, MEN.
Lathyrus sulfureus Brewer ex A. Gray var. *argillaceus* Jepson. SHA, TEH.
Lathyrus tracyi Bradshaw. GLE, MEN, SIS, TRI.

- Lotus yollabolliensis* Munz. HUM, TRI; A-4.
Lupinus antoninus Eastwood. MEN, TEH, TRI; A-1.
Lupinus aridus Douglas ex Lindley subsp. *ashlandensis* Cox. JAC; B-1a, C, D-1.
Lupinus constancei T. W. Nelson & J. P. Nelson. HUM, TRI; A-1.
Lupinus croceus Eastwood var. *croceus*. SIS, TRI.
Lupinus croceus Eastwood var. *pilosellus* (Eastwood) Munz. SHA, SIS, TRI; A-4.
Lupinus lapidicola Heller. DNT, SIS; A-4.
Lupinus milo-bakeri C. P. Smith. MEN; A-1.
Lupinus mucronulatus T. J. Howell var. *mucronulatus*. JOS; B-1b.
Lupinus tracyi Eastwood. DNT, HUM, SIS, TRI; JOS; A-4, B-2b, C, D-2.
Sophora leachiana Peck. CUR, JOS; B-1b, C, D-3.
Trifolium longipes Nuttall subsp. *oreganum* (T. J. Howell) J. Gillett. HUM, SHA, TRI; JOS.
Trifolium longipes Nuttall subsp. *shastense* (House) J. Gillett. DNT, SHA, SIS.

Limnanthaceae

- Limnanthes bakeri* T. J. Howell. MEN; A-1.
Limnanthes floccosa T. J. Howell subsp. *bellingeriana* (Peck) Arroyo. SHA; JAC; A-1, B-2b, C, D-1.
Limnanthes floccosa T. J. Howell subsp. *grandiflora* Arroyo. JAC; B-1a, C, D-1.
Limnanthes floccosa T. J. Howell subsp. *pumila* (T. J. Howell) Arroyo. JAC; B-1a, C, D-1.
Limnanthes gracilis T. J. Howell var. *gracilis*. DOU, JAC, JOS; B-1b, C, D-1.

Linaceae

- Hesperolinon adenophyllum* (A. Gray) Small. HUM, LAK, MEN; A-4.
Hesperolinon tehamense H. K. Sharsmith. GLE, TEH.

Malvaceae

- Malacothamnus mendocinensis* (Eastwood) Kearney. MEN; A-1.
Sidalcea malvaeflora (De Candolle) A. Gray ex Benth. subsp. *celata* (Jepson) C. L. Hitchcock. SHA, SIS, TRI.
Sidalcea malvaeflora (De Candolle) A. Gray ex Benth. subsp. *elegans* (Greene) C. L. Hitchcock. DNT, SIS; CUR, JAC, JOS; A-4.
Sidalcea malvaeflora (De Candolle) A. Gray ex Benth. subsp. *nana* (Jepson) C. L. Hitchcock. SIS, TEH; JAC, JOS.
Sidalcea malvaeflora (De Candolle) A. Gray ex Benth. subsp. *patula* C. L. Hitchcock. CUR; B-1b, D-2.
Sidalcea oregana (Nuttall ex Torrey & A. Gray) A. Gray subsp. *eximia* (Greene) C. L. Hitchcock. HUM, MEN, SIS, TRI; CUR, JAC, JOS.
Sidalcea setosa C. L. Hitchcock subsp. *querceta* C. L. Hitchcock. CUR; B-1a, D-1.
Sidalcea setosa C. L. Hitchcock subsp. *setosa*. SIS; CUR, DOU, JAC, JOS; A-4, C, D-3.

Nyctaginaceae

- Mirabilis greenei* Watson. COL, GLE, SHA, SIS, TEH; JAC; D-2.

Onagraceae

- Clarkia amoena* (Lehmann) Nelson & Macbride subsp. *whitneyi* (A. Gray) Lewis & Lewis. HUM, MEN; A-4.
Clarkia borealis E. Small subsp. *borealis*. SHA, TRI; A-4.
Epilobium canum (Greene) Raven subsp. *septentrionale* (Keck) Raven. HUM, MEN, TRI; A-4.

- Epilobium nivium* Brandege. COL, GLE, LAK, MEN, TRI; A-1.
Epilobium oreganum Greene. DNT, HUM, SIS, TEH, TRI; DOU, JOS; A-4, B-1b, C, D-1.
Epilobium rigidum Haussknecht. DNT, SIS; CUR, JAC, JOS; A-4, B-1b, D-2.
Epilobium siskiyouense (Munz) Hoch & Raven. SIS, TRI; JAC; A-1, C, D-2.

Polemoniaceae

- Eriastrum brandegeae* Mason. COL, GLE, LAK; A-1.
Linanthus harknesii (Curran) Greene subsp. *condensatus* Mason. GLE; A-1.
Linanthus nuttallii Milliken subsp. *howellii* Nelson & Patterson. TEH.
Linanthus rattanii (A. Gray) Greene. COL, GLE, LAK, MEN, TEH; A-4.
Navarretia pauciflora Mason. LAK; A-1.
Phlox azurea G. L. Smith. MEN.
Phlox hirsuta E. Nelson. SIS; A-1.

Polygonaceae

- Chorizanthe howellii* Goodman. MEN; A-1.
Eriogonum alpinum Engelm. SIS, TRI; A-1.
Eriogonum congdonii (S. Stokes) Reveal. SHA, SIS, TRI; A-4.
Eriogonum diclinum Reveal. SIS; JOS; A-4, B-1b, D-2.
Eriogonum hirtellum J. T. Howell & Bacigalupi. DNT, SIS; A-4.
Eriogonum kelloggii A. Gray. MEN; A-1.
Eriogonum libertini Reveal. SHA, TEH, TRI; A-4.
Eriogonum pendulum Watson. DNT; CUR, JOS; A-2, B-1b, C.
Eriogonum siskiyouense Small. SIS, TRI; A-4.
Eriogonum ternatum T. J. Howell. DNT, SIS, TEH; CUR, JOS; A-4, D-3.
Eriogonum umbellatum Torrey var. *speciosum* (Drew) S. Stokes. DNT, SIS.

Portulacaceae

- Claytonia saxosa* Brandege. HUM, LAK, MEN, SIS.
Lewisia cotyledon (Watson) Robinson in A. Gray subsp. *cotyledon*. DNT, SIS, TRI; JAC, JOS.
Lewisia cotyledon (Watson) Robinson in A. Gray subsp. *heckneri* (Morton) Munz. SIS, TRI; A-1.
Lewisia cotyledon (Watson) Robinson in A. Gray var. *howellii* (Watson) Jepson. DNT, HUM, SIS, TRI; CUR, DOU, JAC, JOS; A-3, C.
Lewisia cotyledon (Watson) Robinson in A. Gray var. *purdyi* Jepson. CUR, JOS; C, D-1.
Lewisia oppositifolia (Watson) Robinson in A. Gray. DNT; CUR, JAC, JOS; A-1, B-1b, C, D-2.
Lewisia stebbinsii Gankin & Hildreth. MEN, TRI; A-1.

Ranunculaceae

- Delphinium decorum* Fischer & Meyer subsp. *tracyi* Ewan. COL, GLE, HUM, MEN, LAK, TEH, TRI; CUR, JAC, JOS.
Ranunculus austro-oreganus Benson. JAC; C, D-3.

Rhamnaceae

- Ceanothus pumilus* Greene. DNT, HUM, MEN, SIS, TRI; CUR, JAC, JOS.

Rosaceae

- Holodiscus discolor* (Pursh) Maximowicz var. *delnortensis* Ley. DNT, SIS, TRI; JOS.
Horkelia bolanderi A. Gray subsp. *bolanderi*. COL, LAK.

- Horkelia daucifolia* (Greene) Rydberg subsp. *daucifolia*. SIS, TEH, TRI; JAC.
Horkelia daucifolia (Greene) Rydberg subsp. *latior* Keck. TRI.
Horkelia hendersonii T. J. Howell. JAC; B-1b, C, D-1.
Horkelia sericata Watson. DNT, HUM; CUR, JOS; A-2.
Ivesia pickeringii Torrey ex A. Gray. SIS, TRI; A-1.
Potentilla glandulosa Lindley subsp. *globosa* Keck. DNT, HUM, SIS; CUR, JAC, JOS; D-2.
Rubus leucodermis Douglas ex Torrey & A. Gray var. *trinitatis* Berger. TRI.

Rubiaceae

- Galium ambiguum* Wight var. *siskiyouense* Ferris. DNT, HUM, MEN, SIS, TRI; CUR, DOU, JOS.
Galium glabrescens (Ehrendorfer) Dempster & Ehrendorfer subsp. *glabrescens*. DNT, SIS, TRI.
Galium glabrescens (Ehrendorfer) Dempster & Ehrendorfer subsp. *josephinense* Dempster & Ehrendorfer. JOS.
Galium serpenticum Dempster subsp. *scotticum* Dempster & Ehrendorfer. SIS, TRI; A-1.

Salicaceae

- Salix delnorticus* C. K. Schneider. DNT; JOS; A-4, B-1b, D-2.
Salix tracyi Ball. DNT, HUM; CUR, JAC, JOS; A-4, B-1b, D-2.

Saxifragaceae

- Bensoniella oregona* (Abrams & Bacigalupi) Morton. HUM; CUR, DOU, JOS; A-1, C, D-3.
Heuchera pringlei Rydberg. DNT, SIS.
Saxifraga fragarioides Greene. DNT, HUM, SIS, TRI; CUR, JAC, JOS.

Scrophulariaceae

- Antirrhinum subcordatum* A. Gray. COL, GLE, LAK, TEH; A-4.
Castilleja brevilobata Piper. DNT, SIS; JOS; A-4.
Castilleja elata Piper. DNT, SIS; CUR, JOS; A-2.
Castilleja mendocinensis (Eastwood) Pennell. MEN; A-1.
Castilleja schizotricha Greenman. SIS; JAC; A-4.
Collinsia linearis A. Gray. DNT, HUM, SIS, TRI; JAC, JOS.
Cordylanthus tenuis A. Gray subsp. *pallescens* (Pennell) Chuang & Heckard. SIS; A-1.
Mimulus brachiatus Pennell. LAK; A-3.
Mimulus primuloides Benthham var. *linearifolius* Grant. SHA, SIS, TRI.
Orthocarpus castillejoides Benthham var. *humboldtiensis* Keck. HUM; A-1.
Orthocarpus erianthus Benthham var. *gratiosus* Jepson & Tracy. DNT, HUM, MEN; CUR, JOS.
Orthocarpus pachystachys A. Gray. SIS; A-1.
Pedicularis howellii A. Gray. SIS; JOS; A-4, B-1b, C, D-3.
Penstemon anguineus Eastwood. DNT, GLE, HUM, MEN, SIS, TRI; CUR, DOU, JAC, JOS.
Penstemon filiformis (Keck) Keck. SHA, TRI; A-1.
Penstemon newberryi A. Gray subsp. *berryi* (Eastwood) Keck. DNT, GLE, HUM, SIS, TRI; CUR, JOS.
Penstemon purpusii Brandegee. COL, GLE, HUM, LAK, MEN, TEH, TRI; A-4.
Penstemon tracyi Keck. SIS, TRI; A-1.
Synthyris missurica (Rafinesque) Pennell subsp. *hirsuta* Pennell. DOU; B-1a, C, D-1.
Veronica copelandii Eastwood. SIS, TRI; A-4.

Umbelliferae

- Eryngium constancei* Sheikh. LAK; A-1.
Ligusticum californicum Coulter & Rose. DNT, GLE, HUM, MEN, SIS, TRI.
Lomatium cookii J. S. Kagan. JAC.
Lomatium engelmannii Mathias. MEN, SIS, TRI; CUR, JOS; A-4, B-1b, D-2.
Lomatium howellii (Watson) Jepson. DNT, SIS; CUR, JOS; A-4, B-1b.
Lomatium tracyi Mathias & Constance. HUM, SHA, SIS, TEH, TRI; A-4, B-1b, D-2.
Perideridia leptocarpa Chuang & Constance. SIS; A-4.
Sanicula peckiana Macbride. DNT; CUR, JOS; A-4.
Sanicula tracyi Shan & Constance. HUM, TEH, TRI; JOS; A-1, B-1b, C.
Tauschia glauca (Coulter & Rose) Mathias & Constance. DNT, HUM, TRI; CUR, DOU, JAC, JOS; A-4.
Tauschia howellii (Coulter & Rose) Macbride. SIS; CUR, JAC; A-1, B-1b, C, D-1.

Violaceae

- Viola lanceolata* Linnaeus subsp. *occidentalis* (A. Gray) Russell. DNT; CUR, DOU, JOS; A-1, B-1b, C, D-2.
Viola macloskeyi Lloyd subsp. *pallens* (Banks ex De Candolle) M. S. Baker. SIS.

MAGNOLIOPHYTA: LILIOPSIDA

Gramineae

- Calamagrostis foliosa* Kearney. DNT, HUM, MEN; A-1.
Lophochlaena californicus Nees var. *davyi* (L. Benson) Löve. LAK, MEN.
Poa piperi Hitchcock. DNT, SIS; CUR, JOS; A-4, B-1b, C, D-2.

Iridaceae

- Iris bracteata* Watson. DNT; CUR, JOS; A-2.
Iris innominata Henderson. DNT; COS, CUR, DOU, JOS; A-2.
Iris tenax Douglas subsp. *klamathensis* Lenz. HUM, SIS; A-4.

Liliaceae

- Allium fimbriatum* Watson var. *purdyi* (Eastwood) Ownbey & Aase. COL, LAK; A-4.
Allium hoffmanii Ownbey. HUM, SHA, TEH, TRI; A-4.
Allium mirabile Henderson. DOU.
Allium siskiyouense Ownbey. DNT, HUM, SIS, TRI; CUR, DOU, JAC, JOS; A-4.
Brodiaea coronaria (Salisbury) Engler subsp. *rosea* (Greene) Niehaus. LAK, TEH; A-1.
Calochortus greenii Watson. SHA, SIS; JAC; A-1, B-1b, C, D-1.
Calochortus howellii Watson. DOU, JOS; C, D-1.
Calochortus indecorus Ownbey & Peck. JOS; C, D-1.
Calochortus monanthus Ownbey. SIS; A-1.
Calochortus nudus Watson var. *shastensis* (Purdy) Jepson. SIS; A-3.
Calochortus persistens Ownbey. SIS; A-1.
Camassia howellii Watson. CUR, JAC, JOS.
Chlorogalum pomeridianum (De Candolle) Kunth var. *minus* Hoover. TEH.
Dichelostemma ida-maia (Wood) Greene. DNT, HUM, LAK, MEN, SHA, TRI; CUR, DOU, JOS.
Dichelostemma venustum (Greene) Hoover. DNT, HUM, MEN, SHA, SIS, TRI; DOU; A-4.
Disporum parvifolium (Watson) Britton. DNT; CUR, JOS.
Erythronium citrinum Watson. DNT, SIS; CUR, JOS; A-4, B-1b.

- Erythronium hendersonii* Watson. DNT, SIS; JAC, JOS; A-3.
Erythronium howellii Watson. DNT; CUR, JOS; A-4, B-1b, D-2.
Fritillaria adamantina Peck. DOU, JAC; B-1b.
Fritillaria gentneri Gilkey. JAC, JOS; B-1b, C, D-1.
Fritillaria glauca Greene. DNT, GLE, HUM, LAK, TRI; CUR, DOU, JAC, JOS; D-2.
Hastingsia atropurpurea Becking. JOS.
Hastingsia bracteosa Watson. JOS; B-1b, C, D-1.
Lilium bolanderi Watson. DNT, HUM, MEN, SIS; CUR, JAC, JOS; A-4, B-1b.
Lilium kelloggii Purdy. DNT, HUM; JOS.
Lilium occidentale Purdy. HUM; COS, CUR; A-1, B-1b, C, D-1.
Lilium vollmeri Eastwood. DNT, HUM, SIS; CUR, JAC, JOS; A-3, C.
Lilium wigginsii Beane & Vollmer. DNT, SIS; JAC; A-3, B-1b, C.
Trillium ovatum Pursh subsp. *oettingeri* Munz & Thorne. SHA, SIS, TRI; A-4.
Trillium rivale Watson. DNT, SIS; CUR, DOU, JOS; A-4.
Triteleia crocea Greene var. *crocea*. DNT, SHA, SIS, TRI; CUR, JAC, JOS; A-4.
Triteleia crocea Greene var. *modesta* (Hall) Hoover. SHA, SIS, TRI; A-4.
Triteleia hendersonii Greene var. *leachiae* (Peck) Hoover. CUR; D-2.

Smilacaceae

- Smilax jamesii* Wallace. DNT, SHA, SIS, TRI; A-4.

ANNOUNCEMENT

NEW PUBLICATION

WALTERS, D. R. and D. J. KEIL. 1988. *Vascular plant taxonomy*, 3rd ed., Kendall/Hunt Publishing Co., Dubuque, Iowa, 1988, 488 pp., illus., ISBN 0-8403-4614-X, \$39.95 (paperbound). [Text for introductory level taxonomy classes, completely rewritten and expanded from 2nd edition. Organized in four sections: Part I, Basics of Introductory Taxonomy, includes nomenclature, vegetative terminology, key construction, introduction to manuals and floras, and plant collecting. Part II, Survey of Vascular Plant Families, includes chapters on ferns and fern allies, gymnosperms, and eleven chapters on angiosperms organized according to Cronquist's 1981 system of classification. Families receiving greatest emphasis are illustrated with original line drawings, floral diagrams, and floral formulas. Part III, Approaches to Classification, briefly surveys character variation, artificial and phenetic systems, traditional phylogenetic systems, and cladistics. Part IV, Gathering and Analysis of Data, examines experimental taxonomy and the preparation of revisions and monographs. The book includes a key to many but not all plant families and a detailed glossary.]

NOTES

NOMENCLATURE OF *Lomatium nuttallii*, *L. kingii*, AND *L. megarrhizum* (API-ACEAE).—The recent new combination of *Lomatium kingii* by Cronquist (Great Basin Nat. 46:254, 1986) prompted a routine review of the nomenclature of *Lomatium nuttallii* (Gray) Macbr., *L. megarrhizum* (A. Nels.) Mathias, and *L. kingii* (Wats.) Cronq. in preparation by the senior author for an upcoming revision of *Manual of the Vascular Plants of Wyoming*. The oldest name in the group is *Seseli nuttallii* Gray (Proc. Amer. Acad. Arts 8:287, 1870). Gray cited two collections (syntypes) in his original description, one from the Rocky Mountains (*Nuttall s.n.*), and the other from the Huerfano Mountains, New Mexico (actually Colorado—see *Rhodora* 60:265–271, 1958) (Parry 83). The Nuttall collection is what has recently been called *L. megarrhizum*. The Parry collection is the holotype of *Neoparrya lithophila* Mathias.

It is first necessary to typify the name *Seseli nuttallii*, because current usage is incorrect. Gray's original description included both the Nuttall and Parry collections so both have equal standing for a lectotype. Watson (Proc. Amer. Acad. Arts 22:474, 1887) was the first to deal with Gray's name when he placed the Nuttall collection cited by Gray into synonymy with *Peucedanum kingii* Wats., a new name for *P. graveolens* Wats. that was reputedly a later homonym. (*P. nuttallii* was preoccupied so a transfer could not be made.) The type of *P. graveolens*, and therefore of *P. kingii*, is not the same taxon as the Nuttall collection, however. Watson was not sure what the Parry collection was. We will return to the Watson names later.

Coulter and Rose (Revision of North American Umbelliferae 71, 1888) were next to deal with the problem. They used the name *Peucedanum kingii* Wats., with *P. graveolens* Wats. and *Seseli nuttallii* Gray "in part" in synonymy. *Seseli nuttallii* was not treated elsewhere in their paper. This is no change from Watson's treatment. In their 1900 revision (Contr. U.S. Natl. Herb. 7:245) they used the name *Cynomarathrum nuttallii* (Gray) C. & R. with the following in synonymy: *Seseli nuttallii* Gray, *Peucedanum graveolens* Wats., *P. kingii* Wats., and *P. megarrhiza* A. Nels. The epithet "nuttallii" was not preoccupied in *Cynomarathrum* as it was in *Peucedanum*. The type locality was given as "Rocky Mountains; collected by Nuttall." Here is the first designation of a lectotype. Subsequent workers (Mathias, Ann. Missouri Bot. Gard. 25:225–297, 1938; Mathias and Constance, North Amer. Fl. 28B(2):161–295, 1945) have followed this designation. Furthermore, Mathias' use (Ann. Missouri Bot. Gard. 16:393–398, 1929) of the Parry specimen as the holotype of *Neoparrya lithophila* left the Nuttall specimen the only remaining element of Gray's *Seseli nuttallii*. The Nuttall specimen then typifies *Seseli nuttallii* Gray, and *Lomatium nuttallii* (Gray) Macbr. becomes the correct name for the species on barren clay hills and flats of Nebraska, Wyoming, and Colorado that previously was known as *L. megarrhizum* (A. Nels.) Mathias.

Now we must deal with Watson's names in *Peucedanum*. Watson first used the name *Peucedanum graveolens* (Watson in King, Rep. Geol. Explor. 40th Parallel 5: 128, 1871), the holotype being *Watson 463* from the Wasatch Mountains of Utah at around 9000 feet. He later discovered that Bentham and Hooker had apparently used the same name in 1867 (Genera Plantarum 1:919) for a different taxon, so he proposed the new name of *P. kingii* (Proc. Amer. Acad. Arts 22:474, 1887) for his species. In examining the Bentham and Hooker publication, we discovered that the name *Peucedanum graveolens* had in fact not been used by them. They simply listed *A. graveolens* (*Anethum*) under the genus *Peucedanum*, which is not a valid transfer. The International Code of Botanical Nomenclature is very clear on this point as it has an example (Article 33.1, Ex. 2) from this very same publication. *Peucedanum graveolens* Wats., therefore, is legitimate, and *P. kingii* Wats. is superfluous. *Peucedanum gra-*

veolens Wats. is the oldest name for the species that has been called *Lomatium nuttallii* and, therefore, must be transferred.

The nomenclature of the entire group follows.

LOMATIUM NUTTALLII (Gray) Macbr., Contr. Gray Herb. 56:35. 1918. — *Seseli nuttallii* Gray, Proc. Amer. Acad. Arts 8:287. 1870. — *Cynomarathrum nuttallii* (Gray) C. & R., Contr. U.S. Natl. Herb. 7:245. 1900. — *Cogswellia nuttallii* (Gray) Jones, Contr. W. Bot. 12:32. 1908. — *Aletes nuttallii* (Gray) Weber, Phytologia 55:6. 1984. — LECTOTYPE by Coulter and Rose (Contr. U.S. Natl. Herb. 7:245. 1900): Rocky Mountains, *Nuttall s.n.* (GH!, photo UC!; isolectotype: NY!, photo RM!).
Peucedanum megarrhiza A. Nels., Bull. Torrey Bot. Club 26:130. 1899. — *Cynomarathrum megarrhizum* (A. Nels.) Rydb., Flora Rocky Mountains 629, 1064. 1917. — *Lomatium megarrhizum* (A. Nels.) Mathias, Ann. Missouri Bot. Gard. 25: 282. 1938, issued 1937. — *Neoparrya megarrhiza* (A. Nels.) Weber, Phytologia 41:487. 1979. — *Aletes megarrhiza* (A. Nels.) Weber, Phytologia 55:6. 1984. — LECTOTYPE by Mathias (Ann. Missouri Bot. Gard. 25:282. 1938, issued 1937): Wyoming, Point of Rocks, *Nelson 4769* (RM!; isolectotype: GH!, MO!, NY, photo RM!, US).

***Lomatium graveolens* (Wats.) Dorn & Hartman, comb. nov.** — *Peucedanum graveolens* Wats. in King, Rep. Geol. Explor. 40th Parallel 5:128. 1871. — *Peucedanum kingii* Wats., Proc. Amer. Acad. Arts 22:474. 1887 (*nomen superfl.*). — *Lomatium kingii* (Wats.) Cronq. [in Welsh], Great Basin Nat. 46:254. 1986. — HOLOTYPE: Utah, Wasatch (as Wahsatch) Mountains, *Watson 463* (US, photo RM!; isotype: NY!, photo RM!).

LOMATIUM GRAVEOLENS var. ***alpinum*** (Wats.) Dorn & Hartman, comb. nov. — *Peucedanum graveolens* var. *alpinum* Wats. in King, Rep. Geol. Explor. 40th Parallel 5:129. 1871. — *Peucedanum kingii* var. *alpina* (Wats.) C. & R., Revision of North American Umbelliferae 71. 1888. — *Cynomarathrum alpinum* (Wats.) C. & R., Contr. U.S. Natl. Herb. 7:245. 1900. — *Cogswellia nuttallii* var. *alpina* (Wats.) Jones, Contr. W. Bot. 12:32. 1908. — *Lomatium alpinum* (Wats.) Macbr., Contr. Gray Herb. 56:35. 1918. — *Lomatium nuttallii* var. *alpinum* (Wats.) Mathias, Ann. Missouri Bot. Gard. 25:279. 1938, issued 1937. — *Lomatium kingii* var. *alpinum* (Wats.) Cronq. [in Welsh], Great Basin Nat. 46:255. 1986. — HOLOTYPE: Nevada, East Humboldt Mountains, *Watson 464* (US, photo RM!; isotypes: GH!, NY!, photo RM!).

NEOPARRYA LITHOPHILA Mathias, Ann. Missouri Bot. Gard. 16:393. 1929. — *Aletes lithophila* (Mathias) Weber, Phytologia 55:5. 1984. — HOLOTYPE: Colorado (as New Mexico), Huerfano (as Huefano) Mountains, *Parry 83* (GH, photo Ann. Missouri Bot. Gard. 16:pl. 33, after p. 398. 1929!; isotype: MO!).

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NOTEWORTHY COLLECTIONS

COLORADO

ANTENNARIA AROMATICA Evert (ASTERACEAE).—Gunnison Co.: Cottonwood Pass, about 0.5 mi s. of hwy., rocky slopes, mostly nw.-facing fell fields, T14S R81W S14, 3877 m, 1 Aug 1984, *Bayer et al. CO-449* (RM); Cumberland Pass, rt. 765, T51N R4E, 1 Aug 1984, *Bayer et al. CO-441* (RM); sw. summit of Galena Peak, T12S R87W S11, 3749 m, 31 Jul 1984, *Bayer et al. CO-435* (RM). Summit Co.: Hoosier Pass area, 0.25 mi s. of Hoosier Pass, T8S R78W S10, 2 Aug 1984, *Bayer et al. CO-458* (RM), (verified by R. Bayer). Pitkin Co.: Taylor Pass, Jul 1986, *K. Matthews s.n.* (verified by W. A. Weber). Lake Co.: Sawatch Mts., Mt. Champion Basin, fell field adj. to old mine, granitic substrate, 3751 m, 20 Aug 1986, *Hartman and Rottman 6671/2942* (COLO, CU—Denver) (verified by W. A. Weber). In CO, the species occurs in fell fields of calcareous rocks in the alpine.

Significance. First records for CO and a range extension of ca. 610 km sse. of the nearest localities at 21 km sw. and 8 km w. of Cody, Park Co., WY (Evert, Madroño 31:109–112, 1984). The species also is known from mountainous areas of w. central (Cascade Co.) and sw. (Gallatin and Carbon cos.) MT (verified by W. A. Weber).—STEVE L. O'KANE, JR., Colorado Natural Areas Program, 1313 Sherman St., Room 718, Denver, CO 80203; EMILY L. HARTMAN and MARY LOU ROTTMAN, Biology Dept., Univ. Colorado, Denver 80202.

ARALIA RACEMOSA L. (ARALIACEAE).—La Plata Co.: Elbert Ck, 1.2 mi sw. of confluence of Sawmill Creek and the Animas River, T38N R8W S31, 2290 m, 26 Jul 1986, *W. Baker and D. Paulson s.n.* (COLO, CS).

Significance. First record for CO, a range extension of ca. 150 km n. from the nearest locality in Rio Arriba Co., NM.

ASTRAGALUS HUMILLIMUS A. Gray ex Brand. (FABACEAE).—Montezuma Co.: n. rim of unnamed mesa between Tanner Mesa and Short Mesa, on exfoliating Point Lookout sandstone, T33N R17W S22, 1859 m, 14 May 1986, *O'Kane 2342* (COLO).

Significance. First CO record of this federally endangered species (Fed. Reg. 50: 26568–26572, 1985) since the type collection was made in 1875. This collection came from a population growing under conditions similar to those reported by Brandegee (Bull. U.S. Geol. Surv. Terr. 2:235, 1876) as “growing upon sandstone rock of the Mesa Verde, near the edge of Mancos Canyon.” The nearest known locality is 31 km se. in San Juan Co., NM.

ASTRAGALUS SERICOLEUCUS A. Gray (FABACEAE).—Chaffee Co.: Harrington Gulch, w. of Salida and above and s. of Adobe Park, barren hills of alluvium with *Pinus* and *Cercocarpus*, T50N R8E S35, 2225 m, 1 Aug 1985, *O'Kane and Anderson 2217* (NY) (verified by R. C. Barneby).

Significance. Range extension of 260 km w. of the nearest locality on the plains in Lincoln Co. (Barneby, *Memoirs N.Y. Bot. Gard.* 13:1144–1146, 1964). Two rare endemics restricted to sedimentary strata in the Cañon City area also occur at this site. These species, *Eriogonum brandegei* Rydb. (Reveal, A revision of the genus *Eriogonum*. Ph.D. diss., Brigham Young Univ., 1969) and *Parthenium tetraeuris* Barneby (Rollins, *Contr. Gray Herbarium* 172:1–72, 1950), grow at least 440 m higher than at locations below the mouth of the Canyon of the Arkansas River. Also, *Neoparrya lithophila* Mathias grows here on a sedimentary, rather than igneous substrate.

ATRIPLEX PLEIANTHA W. A. Weber (CHENOPODIACEAE).—Montezuma Co.: 2.2 mi due e. of jct. of Hwys. 160 and 41 in gray clays derived from Mancos shale, T32N R19W S8, 1493 m, 8 May 1985, *O'Kane, Anderson and Fleming 2022* (CS).

Significance. Re-collection of type locality and first collection from CO since 1949 (*Weber 4788*, COLO). This species is a candidate for federal listing as endangered or threatened (Fed. Reg. 50:39534, 1985).

CREPIS CAPILLARIS (L.) Wallr. (ASTERACEAE).—Larimer Co.: Dixon Reservoir, 1 mi se. of Dixon Canyon Dam, T7N R69W S29, 1585 m, 8 Aug 1986, *D. Wilken 14676* (COLO, CS, RM).

Significance. First record for CO, adventive and presumably a range extension w. from the eastern Great Plains (Barkley, Asteraceae, *In Flora of the Great Plains*, Univ. Kansas Press, 1986).

CRYPTANTHA WEBERI I. M. Johnston (BORAGINACEAE).—Conejos Co.: "Flat Top" Mountain in San Luis Hills, sides of mesa in dark volcanic rocks with *Artemisia*, *Bouteloua*, and *Pinus*, T34N R11E S8, 2682 m, 10 Jul 1986, *O'Kane and Anderson 2503* (CS).

Significance. Range extension of 111 km se. from a small area of endemism in Saguache and Hinsdale cos. (Higgins, Brigham Young Univ. Science Bull. 13:1-63, 1971).

DITHYREA WIZLIZENII Engelm. (BRASSICACEAE).—Montezuma Co.: Along Cowboy Wash, 2 mi e. of Utah State Line, T32N R20W, 27 Apr 1985, *Fleming s.n.* (SJNM).

Significance. First modern collection of the species from CO. Some doubt exists whether Brandegee's report from the "valley of the San Juan" (Bull. U.S. Geol. Surv. Terr. 2:233, 1876) was actually from CO or UT (*Weber*, Univ. Colo. Studies, Biology 23:7, 1966).

IPOMOPSIS CONGESTA (Hook.) V. Grant subsp. CREBRIFOLIA (Nutt.) Day (POLEMONIACEAE).—La Plata Co.: 0.3 mi ne. of La Boca on Shellhammer Ridge, T32N R7W S15, 1 May 1985, *O'Kane 85-39* (CS).

Significance. First record for CO. Previously known from sw. MT and n. WY to NM and UT (Cronquist et al., Intermountain Flora 4:128, 1985) and recently reported from NV (Tiehm, Madroño 33:228, 1986). Range extension of ca. 200 km n. of Sandoval Co., NM and ca. 180 km e. of San Juan Co., UT.

LOMATIUM BICOLOR (S. Wats.) Coult. & Rose var. BICOLOR (APIACEAE).—Gunnison Co.: Snowshoe Mesa, abundant on clay loam with *Wyethia* sp., sagebrush, and oak, T13-T14S R89W, 2590 m, 18 Jul 1938, *F. E. Read R-406* (USFS) (verified by M. Schlessman).

Significance. First record for CO; a range extension of ca. 430 km to se. from Salt Lake Co., UT and Lincoln Co., WY. Variety *leptocarpum* (Nutt. ex Torr. & Gray) Schlessman is known from Gunnison Co. (Schlessman, Syst. Bot. Monogr. 4:26-28, 1984).

MENTZELIA DENSE Greene (LOASACEAE).—Fremont Co.: 2.0 road mi e. of Cotopaxi on Hwy. 50, Arkansas River Canyon, T48N R12E S29, 1951 m, 31 Jul 1985, *O'Kane and Anderson 2204* (CS).

Significance. Relocation of the most recent collection of the species (*H. Thompson 1684*, LA, US) made in 1955. The species is limited to the Arkansas River Canyon from Cañon City to Cotopaxi. Darlington (Annals Mo. Bot. Gard. 21:157-158, 1934) enigmatically reports the species from "southern Colorado" with specimens from "Mesa County." Specimens examined by Darlington are probably best ascribed to *M. multiflora* (Nutt.) Gray. Darlington does not indicate that the species is found in the Arkansas Canyon, although Greene (Pittonia 3:99, 1896) states that it is "common" here.

NEOPARRYA LITHOPHILA Mathias (APIACEAE).—Chaffee Co.: on county road 111A, ca. 0.8 km s. of Salida, T49N R9E S7, 2217 m, 2 Aug 1985, *O'Kane and Anderson* 2218 (COLO, CS), *Anderson 85-110* (RM). Conejos Co.: Flat Top, San Luis Hills, T34N R11E S8, 2682 m, 10 Jul 1986, *O'Kane, Anderson, and Dixon* 2500 (COLO, CS). Rio Grande Co.: Elephant Rocks, 8 km ne. of Del Norte, T40N R6E S3, 2423 m, 25 Jul 1984, *J. Anderson s.n.* (RM), 24 Jul 1985, *B. C. Johnston* 3038 (RM), 3041 (COLO, RM); T40N R6E S4, 24 Jul 1985, *Johnston* 3051 (COLO, RM). Saguache Co.: Middle Creek, 3048 m, 10 Jul 1922, *C. E. Taylor* 475 (USFS); ca. 0.8 air km w. of Upper Saguache Forest Service Station, T45N R5E S19, 2621 m, 18 Sep 1983, *Hartman* 17350 (COLO, CS, RM); Upper Saguache Station, 2621 m, 6 Jul 1922, *Taylor* 476 (USFS); road to Jacks Creek, 0.8 km nw. of jct. of Hwy. 114, T45N R6E S10, 25 Jul 1985, *Johnston* 3062 (RM); road to Middle Creek, 2.4 km nnw. of Hwy. 114, T45N R6E S4, 25 Jul 1985, *Johnston* 3063 (RM); Forest road 660, ca. 2.4 km w. of jct. with Del Norte-La Garita road, T41N R6E S21, 2500 m, 8 Aug 1985, *O'Kane and Anderson* 2241 (CS); hill along Cottonwood Creek, ca. 3.2 km w. of Rio Grande Canal and ca. 8.9 km sw. of Swede Corners, T43N R7E S32, 2408 m, 9 Aug 1985, *O'Kane* 2245 (BRY, CS). Locally occasional to abundant on hills, benches, cliff faces, and boulder fields of Tertiary volcanics with *Artemisia*, *Bouteloua*, *Chrysothamnus*, *Eriogonum*, *Hymenoxys*, *Muhlenbergia*, *Oryzopsis*, *Pinus ponderosa*, *Pseudotsuga*, *Ribes*, and *Symphoricarpos*. *O'Kane and Anderson* 2218 is unusual in being abundant on barren, near-white, silt-loam alluvium of the Dry Union Formation.

Significance. Range extension of 82 km sw. or 110–130 km w. to nw. of the only previously published locality (type locality?) at Silver Mt. (as Dike Mt., Weber, *Rhodora* 60:265–271, 1958), in w. Huerfano Co., CO. The two collections by Taylor, both in late flowering and early fruiting condition, were filed under *Pseudocymopterus anisatus* (A. Gray) Coult. & Rose when discovered by RLH in 1983. *Neoparrya lithophila* is a candidate for federal listing as endangered or threatened (Fed. Reg. 50:39584, 1985), because repeated visits by several workers to Silver Mt. and adjacent areas indicated that it was restricted in distribution. The new records show it scattered along the eastern margin of the San Juan Volcanic Area, a region ca. 15,000 km² in extent and composed of basalts and other volcanics deposited during the early Tertiary. The known altitudinal range is now from ca. 2130 m (Silver Mt. locality) to ca. 3048 m. Theobald, Tseng, and Mathias (*Brittonia* 16:296–315, 1964) note in the species description: “rays . . . reflexed in flower and fruit . . . pedicels . . . reflexed in fruit.” A study of material from all known localities shows that the compound umbels are rounded in early flower with erect to spreading rays (and pedicels), the outer of which become reflexed only with age, thereby often leading to a spherical infructescence.

RUMEX VERTICILLATUS L. (POLYGONACEAE).—Weld Co.: near county road 114, 0.5 mi e. of U.S. Hwy. 85, 7 mi n. of Nunn, 1650 m, 22 Aug 1986, *D. Hazlett* 7527 (CS).

Significance. First record for CO; naturalized and presumably a range extension from e. Kansas (R. Kaul, Polygonaceae, *In* Flora of the Great Plains, Univ. Kansas Press, 1986).—STEVE L. O'KANE, JR., Colorado Natural Areas Program, 1313 Sherman St., Room 718, Denver 80203; DIETER H. WILKEN, Dept. Botany, Colorado State Univ., Ft. Collins 80523; and RONALD L. HARTMAN, Rocky Mountain Herbarium, Univ. Wyoming, Laramie 82071-3165.

REVIEWS

Serpentine and Its Vegetation: A Multidisciplinary Approach. By ROBERT RICHARD BROOKS. 449 pp. Ecology, Phytogeography & Physiology Series Volume 1. T. R.

DUDLEY, General Editor. Dioscorides Press, Portland, OR. 1987. Hardbound. \$47.50. ISBN 0-931146-04-6.

For the dedicated student of plant "serpentine" soil endemism, as well as the casual observer, a book such as this one has long been awaited. Because most botanists lack a strong background in geochemistry and geology, few take the time to wade through the appropriate literature in those fields to develop the needed understanding of the ultramafic environment. Robert Brooks has provided an excellent account on the nature of ultramafic rocks and their derived serpentine soils. The first three chapters outline the geochemistry of ultramafic minerals and their derived soils. Chapters 4-6 review the major works on various aspects of plant endemism on serpentine soils including heavy metal accumulation and nutrient imbalances such as calcium and magnesium. The chapter on plant evolution and serpentine is brief and primarily discusses the evolution of plant groups from a global perspective with little information at the species or population level. Dr. Brooks' expertise and personal bias appears in Chapter 8 with an extensive discussion on plant hyperaccumulation of nickel.

The remaining three quarters of the book are dedicated to the serpentine vegetation of the world. There are eleven vegetation chapters beginning with North America and also including tropical America, northwest Europe, central and southern Europe, continental Asia, Japan, Africa, the Malay Archipelago, New Caledonia, Australia, and New Zealand. Each chapter includes the region's geology, vegetation, and important botanical studies. The book is well-illustrated with maps, tables, graphs, and black-and-white as well as color photographs. The photographs have been reproduced very well and clearly illustrate many interesting plants and places. There are three indices: a subject index, a geographical index, and a botanical index. The botanical index is excellent and includes 2,219 species, subspecies, and varieties of vascular plants, mosses, and lichens. This book has brought together a considerable amount of information; most notable are the many international journal articles. This work will undoubtedly be the main reference source for the serpentine plant literature for some time to come.—NIAL F. MCCARTEN, Dept. Biology, San Francisco State University, San Francisco, CA 94132.

Atlas Cultural de México. Flora. By JERZY RZEDOWSKI and MIGUEL EQUIHUA. 223 pp. Secretaría de Educación Pública, Instituto Nacional de Antropología e Historia, Grupo Editorial Planeta. 1987. \$8400 (pesos).

This volume comprises part of an Atlas Cultural series. Three other volumes have been published to date: Archeology, Tourism, Handicrafts.

The history of Mexico shows that the Mayans, Toltecs, and other early civilizations had a tremendous understanding and appreciation of plants and were successful in cultivating many of them. Urbanization in modern times has resulted in loss of much of this early knowledge and appreciation. It is the authors' hope that this volume will stimulate local peoples' interest in the plants occurring in the many varied habitats of Mexico as well as to enable visitors to become familiar with many of the plants.

The 621 colored photographs presented in the volume constitute less than 2 percent of the flora of Mexico, but they give an excellent idea of the diversity of the native plants in Mexico. Chapters are arranged under nine vegetational categories: 1) Bosque tropical perennifolio, 2) Bosque tropical subcaducifolio, 3) Bosque tropical caducifolio, 4) Bosque espinoso, 5) Matorral xerófilo, 6) Pastizal, 7) Bosque de coníferas y de encinos, 8) Bosque mesófila de montaña, and 9) Vegetación acuática y subacuática. Two maps serve to illustrate this classification. In addition, five more general groups are presented in separate chapters: 10) Algunos otros tipos de vegetación, como la costera y los palmares, 11) Las malezas, 12) Las plantas del hombre, su historia en México, 13) Plantas que caracterizan específicamente la flora mexicana, and 14) La flora patrimonio de México y del mundo. For each plant illustrated there is a brief description, general distribution, common name, flowering period, uses, and the

highway routes (as shown on an introductory map) where one might expect to see it. Each of these chapters is prefaced with a brief discussion characterizing the vegetational type. Where appropriate, mention is included of man's impact on the area. That preceding Las Plantas del Hombre tells of the beginning of agriculture, domestication of vegetables and precolumbian agriculture in Mexico. The final two chapters stress the distinctiveness and beauty of the Mexican flora and the importance of conservation and of rational use of land rather than its despoilment. Within each chapter there is neither taxonomic nor alphabetical arrangement of the entries, but rather there are pleasing groupings of the many photographs presented. In such a book, no formal taxonomic arrangement would be practical. The volume ends with a two page glossary and an incomplete index to common names with their scientific equivalents.

The problem of common names, as discussed in the Introduction, is well illustrated in the chapter "El Matorral Xerófilo," the most abundant vegetation type in Baja California. The common name given in the *Flora* for *Olneya tesota* (p. 75) is *palo fierro*, a name applied to that tree in parts of Sonora, but not in southern Baja California where it is aptly called *uña de gato* (cat's claw), and where *palo fierro* is applied to the southern peninsular endemic *Prosopis palmeri*. However, in California and Arizona, the translation "ironwood" refers to *Olneya tesota*. To further confuse the matter, in northern Baja California, California and Arizona, *uña de gato* refers to *Acacia greggii*. Other examples of common name problems in this chapter are: *colorín* (p. 74) which in Baja California refers to *Erythrina flabelliformis*; *pitaya agria* (p. 80) always refers to *Machaerocereus (Stenocereus) gummosus* in Baja California and never to *Lophocereus schottii*; *Palo verde* (p. 82) might be considered a "generic" common name for *Cercidium*, but in Baja California there are four taxa in *Cercidium*, each with its own name: *dipua* for *C. microphyllum*, *palo brea* for *C. praecox*, *palo estribo* for *C. sonorae*, and *palo verde* for *C. floridum* subsp. *peninsulare*. *Torote* (p. 82) is usually applied to species of *Bursera* whereas *Jatropha cuneata* is known as *matacora*. Space limitations in the *Flora* make it impossible, however, to detail such geographic variation in application of common names.

This *Flora* presents an excellent "overview" of the vegetation of Mexico. It merits wide distribution within Mexico and should be readily available to those visiting our neighbor to the south. At the present value of the peso, it is practically a "give-away". It is to be hoped that some adjustment can be made.—ANNETTA CARTER, Herbarium, Department of Botany, University of California, Berkeley 94720.

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17 February 1988

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MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

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REVIEW OF *ERIGERON EATONII* AND ALLIED TAXA (COMPOSITAE: ASTEREA)

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ABSTRACT

Review of morphological attributes and geographic distributions has led to revised circumscriptions for *Erigeron eatonii* and allied taxa, including recognition of one new taxon (*Erigeron eatonii* var. *lavandulus*) and re-establishment of an older one (*E. sonnei*).

"Crazy-quilt" aptly describes the confounding geographic pattern of sometimes marked and, more often, subtle morphological variants that are subsumed by the phrase "*Erigeron eatonii* and allied taxa" (Figs. 1 and 2). Distributions of some of the morphs seem to be strictly determined by particular, often discontinuous substrates; other morphs are more eclectic in choice of habitat. Although pollen grains show quite a range of volumes (6371 to 15,448 cubic micrometers), all chromosome counts for the group are from diploid ($2n = 18$) plants (Solbrig et al. 1969, Keil and Pinkava 1976, Nesom 1978, and counts reported here). [A report of $2n = 36$, as $n = 18$, for *E. eatonii* var. *eatonii* came from a plant referable to *E. tener* A. Gray (NV, White Pine Co., *Breedlove 5815*, DS, DUKE).] Because local populations often show considerable internal uniformity, but vary from one to another, we suspect that apomixis may be contributing to the complexity in a manner similar to that documented by Beaman (1957) for some species of *Townsendia* and by Noyes et al. (1987) in *Erigeron compositus*. All of the taxa treated here seem to be very closely related; they variously intergrade morphologically and may constitute a single, polymorphic species. Overall, the complex pattern of morphology and geography is similar in some ways to that of *Galium multiflorum* Nutt. (cf. Dempster and Ehrendorfer 1965, Cronquist 1984).

There may be other taxa that belong in this rather loosely defined "alliance". Precise circumscription of the "alliance" is beyond the scope of this paper and probably cannot be satisfactorily determined without detailed field-studies, at least, and should benefit from transplant and breeding experiments. For the present we offer a taxonomic

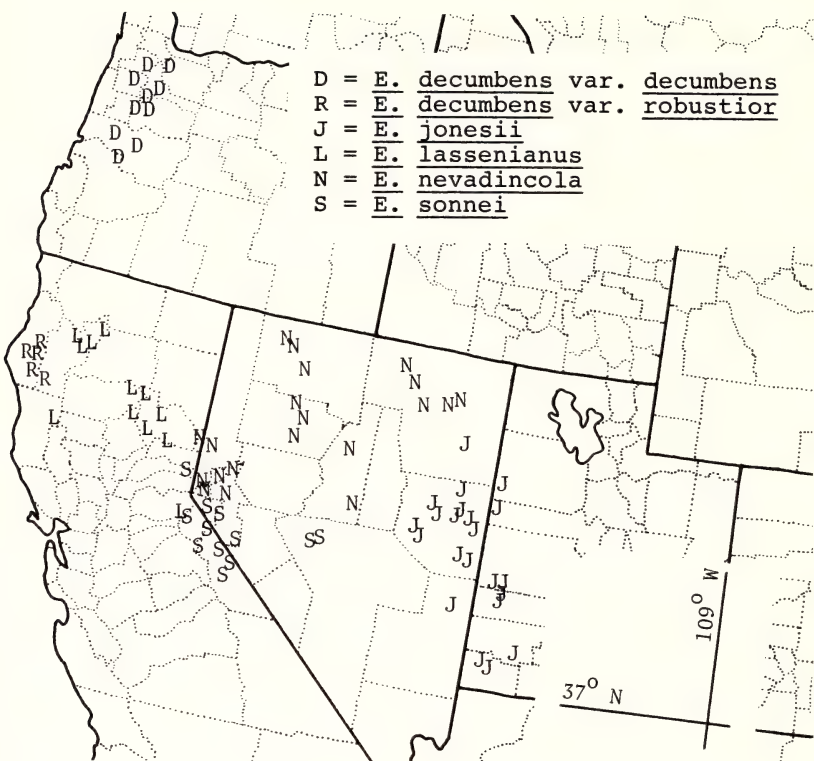


FIG. 1. Distribution of *Erigeron* spp.

"tidying up" based almost wholly on herbarium specimens (ca. 1700 sheets, 25 herbaria).

Treatments of *Erigeron eatonii* and allied taxa in virtually all recent floras are either by Cronquist or derive directly from his excellent revision (Cronquist 1947). Since 1947, however, the numbers of collections of these taxa available for study have perhaps doubled and many of the newer collections fill in gaps in geographic and/or morphologic ranges. Attempts to identify some of these recent collections with Cronquist's keys and descriptions have led us to review the taxonomy of the alliance. As a result, we offer revision of some of his circumscriptions and characterize a previously unrecognized taxon. In assigning ranks to taxa, we have taken a conservative, utilitarian view in order to avoid changes in established nomenclature so far as practicable.

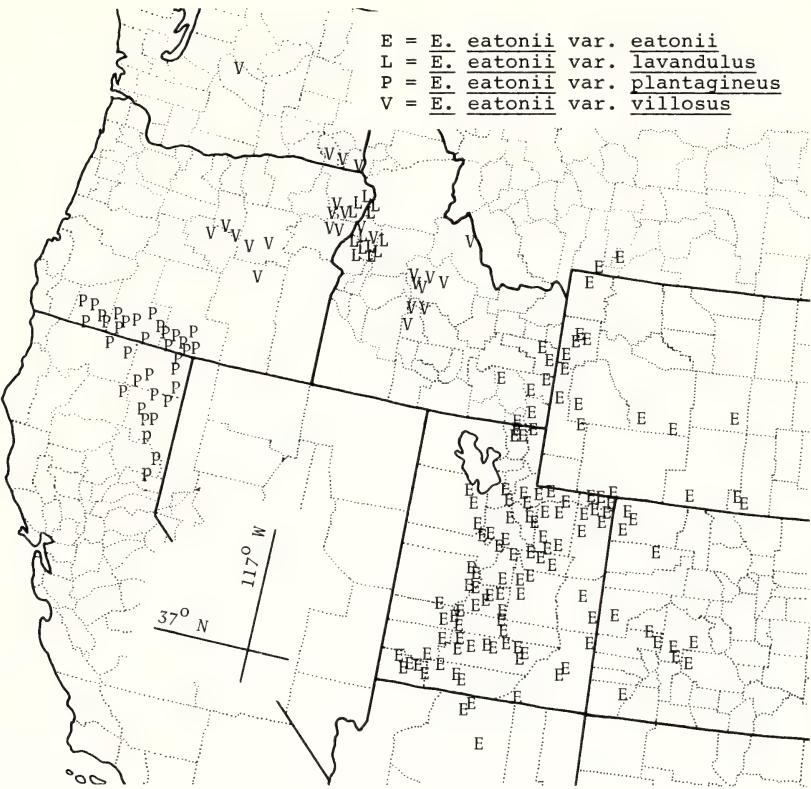


FIG. 2. Distribution of *Erigeron eatonii* subspp.

KEY TO *Erigeron eatonii* AND ALLIED TAXA

- a. Hairs of stems closely appressed or strongly ascending (except peduncles near the heads).
- b. Flowering stems prostrate, decumbent, or erect, 4–15(–30) cm long and bearing 1–2(–7) heads; basal leaves evident at anthesis.
- c. Phyllaries 4–5(–7) mm long; disc corollas 2.5–4(–5) mm long; pappus of 12–18(–28) fragile, barbellulate bristles 2.5–4 mm long plus 6–12 fine setae 0.1–0.5 mm long. 2. *E. eatonii*
- d. Phyllaries moderately to densely glandular-puberulent (may be pilo-hirtellous to villous as well).
- e. Heads 1–2(rarely to 7) per flowering stem, held

- well beyond the basal leaves; shorter phyllaries $\frac{1}{2}$ – $\frac{3}{4}$ as long as the longer; phyllaries sparsely pilo-hirtellous with hairs mostly 0.3–0.8 mm long; Rocky Mts. (AZ, CO, se. ID, MT, UT, WY). 2a. *E. eatonii* var. *eatonii*
- ee. Heads 2–4(1–6) per flowering stem, held just beyond the basal leaves; shorter phyllaries ca. $\frac{3}{4}$ + as long as the longer; phyllaries sparsely to moderately villous with hairs mostly 0.5–1.5+ long; w.-cen. ID, adj. OR. 2b. *E. eatonii* var. *lavandulus*
- dd. Phyllaries sparsely, if at all, glandular-puberulent, variously pilo-hirtellous or villous.
- f. Phyllaries sparsely to moderately pilo-hirtellous with hairs mostly 0.3–0.8 mm long; s.-sw. OR, n.-ne. CA. 2c. *E. eatonii* var. *plantagineus*
- ff. Phyllaries moderately to densely villous with hairs mostly 1–2 mm long; ne. OR, WA, cen. ID. 2d. *E. eatonii* var. *villosus*
- cc. Phyllaries 4.5–10.5 mm long; disc corollas (3.5–)4.5–6.8 mm long; pappus of 20–30 barbellate bristles 4–5 mm long plus 12–20 setae to 1 mm long.
- g. Phyllaries 7–10.5 mm long, length 4.7–6.6 times width; ray floret lamina 7–11 mm long; disc corollas 4.4–6.8 mm long; ne., w.-cen. NV, adj. CA. 5. *E. nevadincola*
- gg. Phyllaries 4.5–8 mm long, length 3.8–5.5 times width; ray floret lamina 4.5–6.6(–8.5) mm long; disc corollas 3.5–5 mm long; border cos. CA–NV and s.-cen. NV. 6. *E. sonnei*
- bb. Flowering stems mostly erect, (15–)30–60 cm long and bearing 2–5(1–18+) heads; basal leaves often withered prior to anthesis. 1. *E. decumbens*
- h. Phyllaries 4–6 mm long; achenes 1.2–1.6 mm long; w. OR. 1a. *E. decumbens* var. *decumbens*
- hh. Phyllaries 6–8.5 mm long; achenes 1.8–2.5 mm long; nw. CA. 1b. *E. decumbens* var. *robustior*
- aa. Hairs of stems patent or retrorse.
- i. Phyllaries 21–32, mostly 4.2–5.6 mm long, length 3.5–5.3 times width; ray florets none or 12–24; CA. 4. *E. lassenianus*
- ii. Phyllaries 36–62, mostly 5.5–7 mm long, length 5–9 times width; ray florets 20–52; e.-cen. NV, sw. UT. [See also

E. eatonii and *E. sonnei*, leads c and gg.].
 3. *E. jonesii*

NOMENCLATURE, DESCRIPTION, AND DISCUSSION

1. *ERIGERON DECUMBENS* Nutt., Trans. Amer. Philos. Soc. ser. 2. 7: 309. 1840 [not *Erigeron decumbens* Eastwood 1906].—TYPE: Nuttall indicated, "Rocky Mountains, towards the Oregon", but Pennell (1936), in reviewing the meager evidence of Nuttall's itinerary in Oregon, reported for late summer of 1835, "a record from 'prairies of the Wahlamet', suggesting that Nuttall had gone . . . up the Willamette valley", *Nuttall s.n.* (Holotype: PH!; isotypes: frag ex BM in DS!; GH fide Cronquist).

1a. *ERIGERON DECUMBENS* Nutt. var. *DECUMBENS*—"Erigeron decumbens Nutt. subsp. *typicus*" Cronquist, *Brittonia* 6:174. 1947.

Stems erect or decumbent only at base, 15–60 cm long, stramineous to reddish at base, sparsely appressed-pubescent; basal leaves often withered before anthesis, linear to very narrowly oblanceolate, the longest 5–12(–18) cm long, 3–4(–9) mm wide; mid-stem leaves mostly linear, 3–9 cm long, 2–4(–8) mm wide; all leaves sparsely to moderately pilo-hirtellous with patent or ascending hairs; flowering stems bearing 2–5(1–18+) heads, these held well beyond the basal leaves, stem/basal-leaf length = 1.8–4.2; involucre broadly hemispheric to rotate, 9–12 mm diam. (pressed); phyllaries 34–47, subequal, linear, length mostly 7–8(6–10) times width, the longest (4.3–)5–6 mm long, often with a strong, orange nerve, sparsely to moderately villous, not glandular; ray florets ca. 35(26–57), corollas white or fading to white from pinkish or pale blue, lamina 7–12 mm long, 1–1.5 mm wide; disc florets ca. 200+, corollas yellow, 3–3.5 mm long; achenes (seldom collected) tan with orange ribs, 1.2–1.6 mm long, sparsely strigillose; pappus of ca. 16 whitish, very fragile bristles ca. 3 mm long plus 8–10+ fine setae ca. 0.1 mm long.

Open grasslands; Oregon: Willamette River drainage (Benton, Clackamas, Lane, Linn, Marion, Polk, and Yamhill cos.); below 300 m; late May to mid-July.

1b. *ERIGERON DECUMBENS* Nutt. var. *ROBUSTIOR* (Cronq.) Cronq. in C. Hitchc. et al., *Vasc. Pl. Pacific Northw.* 5:175. 1955.—*Erigeron decumbens* Nutt. subsp. *robustior* Cronq., *Brittonia* 6:174. 1947.—TYPE: California, Humboldt Co., valley of South Yager Creek, 26 Jun 1932, *J. P. Tracy 10252* (Holotype: UC!; isotype: JEPS!).

Stems erect or decumbent only at the base, 25–55 cm long, stramineous or purplish at base, finely and sparsely appressed-strigillose

or with weakly spreading hairs 0.3–1 mm long, sometimes minutely glandular as well; basal leaves often withered before anthesis, linear to very narrowly oblanceolate, the longest 9–17 cm long, 3–6(–11) mm wide; mid-stem leaves mostly linear, sometimes oblanceolate, 3–6 cm long, 2–5(–11) mm wide; all leaves sparsely pilo-hirtellous with patent or ascending hairs; flowering stems bearing (1–)2–4+ heads, these held well beyond the basal leaves at peak anthesis, stem/basal-leaf length = 1.7–3.1; involucre broadly hemispheric to rotate, 12–18 mm diam. (pressed); phyllaries 30–45, subequal, narrowly lanceolate to linear, length 6–8 times width, the longest 6–8.5 mm long, usually with a strong orange nerve, all moderately to densely villous, little if at all glandular; ray florets 21–36, corollas lilac to deep blue or bluish violet (often fading to white), lamina 7–12(–17) mm long, 1.5–3 mm wide; disc florets 150–200+, corollas yellow, 3.5–4.5 mm long; achenes (seldom collected) tan to greenish with orange ribs, 1.8–2.5 mm long, minutely and sparsely strigillose; pappus of 14–20+ whitish, fragile, barbellulate bristles ca. 4 mm long plus 8–12+ minute setae ca. 0.1 mm long.

Glades and meadows, sometimes associated with serpentine substrates; California (Humboldt and western Trinity cos.; upper drainages of the Eel, Mad, and Van Duzen rivers and headwaters of Redwood Creek); mostly 700–1500 m; early June to late July.

Reports of *E. decumbens* var. *robustior* from Plumas Co., CA, and from Klamath Co., OR, are based on robust specimens of *E. eatonii* var. *plantagineus*.

2. *ERIGERON EATONII* A. Gray, Proc. Amer. Acad. Arts 16:91. 1880.—LECTOTYPE (Cronquist 1947): Utah, Uintah Mountains, on a divide west of Duchesne River and on a ridge above Bear River Canyon, 10,000 feet, Jul 1869, *S. Watson* "546" (Lectotype: GH!; islectotypes: NY!, US!).

2a. *ERIGERON EATONII* A. Gray var. *EATONII*.—"Erigeron eatonii A. Gray subsp. *typicus*" Cronquist, Brittonia 6:172. 1947.

Erigeron microlonchus E. Greene, Pittonia 3:293. 1898.—LECTOTYPE (here designated): "Common on grassy plains and hills of southern Wyoming; collected by the writer plentifully in meadows of Dale Creek . . .", 30 Jun 1896, *E. Greene s.n.* (Lectotype: ND-G, 057127!; islectotype: ND-G, 057128!).

Erigeron eatonii A. Gray f. *molestus* Cronq., Brittonia 6:172. 1947.—TYPE: Utah, Tooele Co., Stansbury Range, east base of Mt. Deseret Peak, 10,000 feet, 23 Jun 1943, *Maguire and Holmgren 21773* (Holotype: NY!; isotype: GH!).

Erigeron canaani Welsh, Great Basin Naturalist 43:366. 1983.—TYPE: Utah, Washington Co., Canaan Mountain, 11 Jun 1980, *J. Anderson s.n.* (Holotype: BRY!; isotype: NY).

Stems prostrate, decumbent, or erect, 9–20(–32) cm long, green,

stramineous, or purplish at base, very sparsely to moderately strigillose with appressed or ascending hairs 0.1–0.8 mm long (rarely with patent hairs); basal leaves linear or very narrowly oblanceolate, the longest 5–10(–18) cm long, 2–5(1–9) mm wide; mid-stem leaves linear, 1–4 cm long, 1–3(–5) mm wide; all leaves moderately strigillose to subglabrous (especially adaxially), hairs appressed to ascending (sometimes erect adaxially), mostly 0.3–0.8 mm long, sometimes longer on basal margins; flowering stems bearing 1–2(–7) heads, these mostly held well beyond the basal leaves, stem/basal-leaf length = (1.1–)1.7–2.8; involucre hemispheric, 10–13(–16) mm diam. (pressed); phyllaries 29–56, linear-oblanceolate, length (4.2–)5–6 times width, the longest 4.5–6 mm long, the outermost 3–6 about half as long as the rest, all moderately to densely glandular-puberulent and sparsely pilo-villous with hairs mostly 0.3–0.8 mm long; ray florets 21–42, corollas white or variously pink, lilac, or lavender, sometimes the pigment more pronounced abaxially and distally, lamina 5–7 mm long; disc florets 80–150+, corollas yellowish to ochroleucous, often tipped with red or purple; achenes grayish tan, 1.7–2.4 mm long, sparsely hairy; pappus of 16–20 fragile, barbel-lulate bristles 3–3.5 mm long plus 12–16 fine setae 0.2–0.5 mm long; $2n = 18$ (Keil and Pinkava 1976, Nesom 1978).

Open or exposed, often meadowy places, with sagebrush, pinyon-juniper, aspen-conifer forests; western Rocky Mts., Arizona (Coconino Co.), Colorado (Eagle, Grand, Gunnison, Mesa, Moffat, Montezuma, Montrose, Rio Blanco, and Saguache cos.), Idaho (Bannock, Bear Lake, Bonneville, Caribou, and Franklin cos.), Montana (Park and Stillwater cos.), Utah (all but Box Elder and Morgan cos.), and Wyoming (Albany, Carbon, Fremont, Lincoln, Natrona, Park, Sweetwater, Sublette, Teton, and Uinta cos.); 1900–2700 (1650–3600) m; mid-May to mid-August.

Some plants from the Stansbury Range in western Utah differ from typical *E. eatonii* in having patent hairs on the stems; in this regard they approach *E. jonesii* (q.v.). Cronquist (1947) called such plants *E. eatonii* f. *molestus*. Other plants from the same area closely match typical *E. eatonii*.

Welsh (1983) based *E. canaani* on plants from southwestern Utah that differ from typical *E. eatonii* primarily in having very narrow leaves with rather long hairs along the proximal margins. Although the habit of these plants is striking, they seem to represent an extreme form of *E. eatonii* var. *eatonii* rather than a distinct taxon. Specimens quite similar to the type of *E. canaani* have been collected elsewhere in the range of var. *eatonii* (e.g., Duchesne Co., Utah, Neese 9341, BRY, NY).

2b. ***Erigeron eatonii* A. Gray var. *lavandulus* Strother & Ferlatte, var. nov.**—TYPE: Idaho, Idaho Co., Seven Devils Mountains, plateau area of Dry Diggins, dry, barren flat, 1 Aug 1952, A. R.

Kruckeberg 3207 (Holotype: UC!; isotypes: NY!, ORE!, RM!, RSA!, UTC!).

Herbae perennes caulibus floriferis foliis basalibus 1–1.5-plo longioribus, phyllariis 26–40 plerumque modice glandulosis tantum parce vel modice villosis (piliis 0.5–1.5 mm longis) raro apicibus rubris, corollis radiorum lavandulis vel purpureis haud subroseis vel erubescensibus raro niveis vel albescentibus.

Stems prostrate to decumbent, 5–12(–22) cm long, closely or loosely strigillose with appressed to weakly spreading hairs 0.1–0.8 mm long, usually minutely glandular as well, at least distally; basal leaves linear to narrowly oblanceolate, the longest 6–9(–17) cm long, 2–4(–7) mm wide; mid-stem leaves linear, 2–4(–8) cm long, 1–2(–4) mm wide; all leaves loosely strigillose; flowering stems bearing 2–4(1–6) heads, these held barely if at all above the basal leaves at peak anthesis, stem/basal-leaf length 1–1.5(–1.9); involucre hemispheric, 9–13 mm diam. (pressed); phyllaries 26–40, subequal or weakly graduate, linear to lanceolate, length mostly 5–6 times width, the longest (4.5–)5–7 mm long, little if at all carinate, usually glandular and sparsely to moderately villous with hairs 0.5–1.5+ mm long, rarely reddish on distal margins and in the minutely erose, attenuate tip; ray florets 25(16–36), corollas deep lavender or bluish-purple, rarely white or fading to white, not pink or reddish, lamina 5.5–8(–9) mm long, 1–2 mm wide; disc florets 100–150+, corollas ochroleucous to yellowish, often tipped with purple, 2.5–3.5(–4) mm long; achenes tan with tan to orange ribs, 1.8–2.2 mm long, very sparsely strigillose; pappus of 12–20 white, fragile, barbellulate bristles 3–3.5 mm long plus 6–9+ minute setae 0.1–0.3 mm long; $2n = 18$ (Solbrig et al. 1969; as *E. eatonii* var. *villosus*).

Open grasslands and meadows, mostly in sagebrush scrub communities on scablands; Idaho (Adams, Idaho, Valley, and Washington cos.) and adjacent Oregon (Union and Wallowa cos.); 900–1850(–2300) m; mid-May to mid-August.

The plants treated here as var. *lavandulus* were included in var. *villosus* by Cronquist. In addition to differences evident in the key, var. *lavandulus* differs from var. *villosus* in having lavender to bluish ray corollas (rarely white or fading to white) vs. usually white (or tinged with pink, not bluish), flowering stems usually bear 2–4+ heads vs. 1 (rarely 2), stem length to basal-leaf length ratio equals 1–1.5(–1.9) vs. 1.7–2.8, and habitat preference is mostly for sagebrush associations vs. lodgepole pine associations.

Note: Three collections from west of the Cascade crest in northern Oregon, some 400 km disjunct from typical var. *lavandulus*, may belong within this circumscription.

1) *T. J. Howell s.n.* [Clackamas Co., “on grassy slopes of the Cascade mountains near Table Rock” (with description), “Rooster

Rock" (on label), 22 Aug 1899, ORE!] is the type of *Erigeron pacificus* Howell [Fl. Northw. Amer. 1(3):319. 1900]. The specimens have suffered considerable insect damage and are difficult to interpret; they are somewhat hairier than is typical of var. *lavandulus*.

2) *L. M. Kemp s.n.* [Clackamas Co., Fish Creek Mtn., 3600 ft, 27 Jul 1979, ORE!, OSC!] has proportionately wider basal leaves and longer flowering stems and has absolutely longer ray corollas (lamina 12–15 mm) than in typical var. *lavandulus*.

3) *G. Whitehead 1905* [Marion Co., Scorpion Mtn., 4800 ft, 28 Jul 1982, ORE!, OSC!] has flowering stems up to twice as long as basal leaves but otherwise fits well within our circumscription of var. *lavandulus*.

Alternative treatments of these collections are: 1) resurrection of *E. pacificus* as a distinct taxon or 2) treatment of *E. pacificus* as taxonomic synonym of *E. eatonii* var. *lavandulus*. A reasonable choice cannot be made from information at hand and must await further studies of plants from eastern Clackamas and Marion counties. It seems certain that the type of *E. pacificus* does not fall within the circumscription of *E. eatonii* var. *villosus* as here drawn.

2c. *ERIGERON EATONII* A. Gray var. *PLANTAGINEUS* (E. Greene) Cronq. in C. Hitchc. et al., Vasc. Pl. Pacific Northw. 5:175. 1955.—*Erigeron plantagineus* E. Greene, Pittonia 3:292. 1898.—*Erigeron eatonii* A. Gray subsp. *plantagineus* (E. Greene) Cronq., Brittonia 6:173. 1947.—LECTOTYPE (here designated): California, Modoc Co., Lava Beds, Jun 1894, *Mrs. R. M. Austin s.n.* [268 in UC] (Lectotype: ND-G, 057228!; isolectotypes: ND-G, 057224!, UC!). Note: Cronquist (1947) cited *Austin s.n.* (ND-G) as type but did not annotate either of the specimens now in ND-G.

Erigeron robertianus E. Greene, Pittonia 3:293. 1898.—TYPE: Oregon, "Roberts' Ranch" (in "southeast Oregon"), 1893, *Mrs. R. M. Austin s.n.* (Holotype: ND-G!).

Stems prostrate to decumbent, 10–23+ cm long, stramineous or somewhat purplish at base, sparsely to moderately strigillose with appressed or slightly spreading hairs 0.2–0.5 mm long, usually somewhat glandular as well; basal leaves linear to narrowly oblanceolate, the longest 5–11(–16) cm long, 3–8(–13) mm wide; mid-stem leaves narrowly oblong to linear, 1.5–3(–5) cm long, 2–4(–8) mm wide; all leaves sparsely to moderately strigillose with closely appressed to weakly spreading hairs on both faces, usually minutely glandular as well; flowering stems bearing 1–4 heads, these held just beyond to well beyond the basal leaves, stem/basal-leaf length = (1.1–)1.5–2.7; involucre broadly hemispheric to subrotate, 11–12(9–14) mm diam. (pressed); phyllaries 31–49, subequal to weakly graduate, linear to lanceolate, length 5–7(4.5–8.5) times width, the longest 5–7

mm long, usually somewhat navicular, little, if at all, glandular, usually sparsely to moderately hirsute or villous with hairs 0.3–0.8 mm long; ray florets 23–39, corollas white or pink to bluish or purple, then often fading to white, lamina 6–8(–13) mm long, 1.5–2 mm wide; disc florets 100–150+, corollas ochroleucous to yellow, often tipped with red in age, 3–4 mm long; achenes (seldom collected) stramineous to orange-tan or puce with stramineous or orange ribs, 1.8–2.3 mm long, sparsely strigillose; pappus of 16–20+ white, fragile, finely barbellulate bristles 3–3.5 mm long plus 6–12 very fine setae 0.1–0.3 mm long; $2n = 18$ (determined from *Strother 1359*, CA, Plumas Co.).

Exposed, often meadowy places, often with sagebrush scrub; usually associated with volcanic/lava substrates, rarely with serpentine (e.g., *Chambers 4358*, Oregon, Jackson Co., Red Mtn.); California (Lassen, Modoc, Plumas, Shasta, and Siskiyou cos.) and Oregon (Jackson, Klamath, and Lake cos.); 1500–2300(1050–2500) m; late May to mid-August.

Robust specimens of *E. eatonii* var. *plantagineus* have been confused with *E. decumbens* var. *robustior*. In Plumas Co., California, *E. eatonii* var. *plantagineus* co-occurs with *E. lassenianus* (cf. *Kearney 153*, US) and specimens intermediate between the two may be found (see discussion of *E. lassenianus*).

- 2d. *ERIGERON EATONII* A. Gray var. *VILLOSUS* (Cronq.) Cronq. in C. Hitchc. et al., *Vasc. Pl. Pacific Northw.* 5:175. 1955.—*Erigeron eatonii* A. Gray subsp. *villosus* Cronq., *Brittonia* 6:172. 1947.—
TYPE: Oregon, “open summit of the Wallowa Mountains”, 2300 m, 29 Jul 1907, *Cusick 3186* [Holotype: NY!; isotypes: GH!, MIN, MO!, ORE(2)!, RM!, UC!, US (2)!, WS].

Stems weakly decumbent to erect, 10–15(5–30) cm long, stramineous or reddish at base, moderately to densely appressed-strigillose with hairs 0.3–0.7 mm long, sometimes minutely glandular as well; basal leaves linear to narrowly oblanceolate, the longest 4–8(–19) cm long, 4–7(2–11) mm wide; mid-stem leaves linear, 2–3(–5) cm long, 1–2(–3) mm wide; all leaves appressed-strigillose, rarely minutely glandular as well; flowering stems bearing 1(–2) heads, these held well beyond the basal leaves at peak anthesis, stem/basal-leaf length = 1.7–2.8; involucre broadly hemispheric to nearly rotate, 12–14(10–17) mm diam. (pressed); phyllaries 28–60, linear to very narrowly oblanceolate, length mostly 5–9.3 times width, the longest 4.5–6.5 mm long, subequal, little if at all carinate, moderately to densely shaggy-villous with white hairs to 0.8–1.5 mm long, usually reddish on distal borders, tips attenuate and minutely erose; ray florets 35(20–50), corollas white, sometimes pinkish, never bluish (rarely bicolored—abaxially pink/adaxially white; e.g., *Maguire 26831* from OR, Grant Co., Strawberry Mtn.), lamina (5–)6–8 mm long,

1–2.5 mm wide; disc florets (60–)90–160, corollas ochroleucous to yellowish, 2.5–3.5 mm long, lobes sometimes with bristle-like hairs; achenes (seldom collected) tan with tan ribs, 1.7–2.2 mm long, sparsely strigillose; pappus of 16–26 white, fragile, barbellulate bristles 2.5–3.5 mm long plus 5–12 very fine setae 0.3–0.5 mm long.

Meadows and open places, often in lodgepole pine forests, sometimes in sagebrush; Idaho (Adams, Blaine, Custer, Idaho, Lemhi, Valley, and Washington cos.), Oregon (Baker, Crook, Grant, Harney, Union, Wallowa, and Wheeler cos.), and Washington (Asotin, Garfield, and Kittitas cos.); 1850–2500(1500–2950) m; mid-June to mid-August.

3. *ERIGERON JONESII* Cronq., Brittonia 6:166. 1947. — TYPE: Nevada, White Pine Co., Aurum, 9 Jul 1891, *M. E. Jones s.n.* (Holotype: POM; isotypes: MO!, NY, ORE!, PH, RM, UC!, US).

Erigeron wahwahensis S. Welsh, Great Basin Naturalist 43:368. 1983. — TYPE: Utah, Beaver Co., Wah Wah Mtns., Pine Grove Pass, ca. 12 miles SSW of Wah Wah Spring, 2450 m, 12 Jun 1982, *S. L. Welsh 21229* (Holotype: BRY!; isotypes: CAS!, GH, MO, NY, POM, RM, US, UT, UTC).

Stems decumbent to ascending or nearly erect, 8–20(–38) cm long, sparsely to densely hirtellous with patent or retrorse hairs 0.1–0.8+ mm long (rarely subglabrous or with ascending hairs); basal leaves spatulate to oblanceolate or linear, the longest 5–8(–17) cm long, 3–8(–19) mm wide, rarely obscurely toothed; mid-stem leaves linear to oblong, often somewhat clasping at base, 1–3(–4) cm long, 4–6(–9) mm wide; all leaves sparsely to moderately pilo-hirtellous with patent or ascending hairs; flowering stems bearing (1–)2–4 heads, these held well beyond the basal leaves at peak anthesis, stem/basal-leaf length = 1.7–3.5; involucre hemispheric to turbinate or subrotate, 12–18 mm diam. (pressed); phyllaries 36–62, subequal or weakly graduate, linear to lance-linear, length mostly 5–7(–9) times width, the longest 5.5–7 mm long, little if at all carinate, somewhat indurate basally, minutely glandular and sparsely to moderately villous; ray florets 34(20–52), corollas whitish, usually with blush of blue or pink distally on abaxial face, rarely colored on adaxial face, lamina 5–7 mm long, 1–2 mm wide; disc florets 150–200+, corollas ochroleucous to yellowish, sometimes tipped with pink or purple, 3–3.5 mm long; achenes grayish tan with pale ribs, 2.2–2.5 mm long, sparsely strigo-hirtellous; pappus of 20–24 whitish, fragile, barbellulate bristles ca. 3 mm long plus ca. 12 fine setae 0.1–0.3 mm long.

Open places, mostly in sagebrush, pinyon-juniper, ponderosa pine, oak-maple, and white fir communities on granitic, limestone, or volcanic substrates; eastern Nevada (Elko, Lincoln, Nye, and White Pine cos.) and adjacent Utah (Beaver, Iron, Juab, Millard, Tooele, and Washington cos.); 2000–2700(–3400) m; late May to mid-August.

Many specimens from various genera and families from southwestern Utah, especially Washington Co., do not "conform" or are unusual within their groups. Welsh (1983) noted that *E. wahwahensis* is "more or less intermediate between phases of *E. eatonii* and *E. jonesii*". We agree that in and near the area where both *E. eatonii* and *E. jonesii* may be found, some specimens are intermediate between the two (e.g., *Atwood 1484* from Washington Co. and *Cottam 3977* from Iron Co.). In the type of *E. wahwahensis*, however, not only is the indument like that of *E. jonesii* but so is the "general aspect".

Pollen volumes in cubic micrometers (μm^3) were determined for five samples of "wahwahensis" from Beaver and Washington cos., UT (6371–7795 μm^3) and for four samples of *E. jonesii* s. str. from Elko and White Pine cos., NV (6710–9097 μm^3). For five samples from *E. eatonii* var. *eatonii* from Colorado, Utah, and Wyoming, the volumes are 6813–7832 μm^3 . These ranges of volumes suggest that polyploidy may occur within species or varieties of this group of erigerons and do not help resolve placement of "wahwahensis".

4. *ERIGERON LASSENIANUS* E. Greene, Fl. Franciscana 389. 1897.—LECTOTYPE (Cronquist 1947): California, Plumas Co., Mt. Dyer, 1880, *Mrs. R. M. Austin s.n.* (Cronquist cited GH and ND-G; we have seen both and take the ND-G specimen to be the lectotype).

Erigeron lassenianus E. Greene var. *deficiens* Cronquist, Brittonia 6:171. 1947.—TYPE: California, Plumas Co., United States Forest Reserve, on trail to Long Valley, 15 Jun 1927, *A. Eastwood 14613* (Holotype: CAS!).

Erigeron flexuosus Cronq., Brittonia 6:174. 1947.—TYPE: California, Trinity Co., Trinity Alps Resort, 25 Jun 1937, *A. Eastwood and J. T. Howell 4903* (Holotype: CAS!).

Stems prostrate to ascending or erect, 9–20(–35) cm long, often somewhat flexuous, mostly stramineous at base, sparsely to densely strigillose to hirtellous with ascending to patent hairs 0.2–0.7 mm long, usually glandular as well, at least on the distal 1–3 internodes (peduncles); basal leaves very narrowly oblanceolate to spatulate or linear, the longest 5–12(–15) cm long, 3–6(–9) mm wide; mid-stem leaves linear to narrowly spatulate, 1–3(–5) cm long, 1.5–3(–5) mm wide; all leaves sparsely to moderately pilo-hirtellous to villous with erect or ascending hairs, often minutely glandular as well; flowering stems bearing (1–)3–7+ heads, these held well beyond the basal leaves at peak anthesis, stem/basal-leaf length = 1.5–3.5; involucre mostly hemispheric, 6–10(–12) mm diam. (pressed); phyllaries 21–32, weakly graduate, oblanceolate, length mostly 3.5–5.3 times width, the longest 4.2–5.6 mm long, all somewhat carinate, minutely granular-glandular and moderately to densely pilo-villous; ray florets none or 21(12–24), corollas pink to lavender or white, lamina 4.5–

8 mm long, 1.5–2.5 mm wide; disc florets 60–90(–120+), corollas ochroleucous to yellowish, sometimes reddish at tip, 2.5–3.5 mm long, lobes often bearing 1–2 bristle-like hairs; achenes tan to greenish brown with stramineous ribs, 1.5–2.3 mm long, very sparsely strigillose; pappus of 12–24 whitish, fragile, barbellulate bristles 1.5–3 mm long plus 8–15 very fine setae 0.1–0.4 mm long; $2n = 18$ (determined from *Strother 1360*, CA, Plumas Co.).

Open places, usually associated with ultramafic (serpentine) or glacial moraine substrates; California (Butte, Eldorado, Lassen, Mendocino, Plumas, Shasta, Sierra, Tehama, and Trinity cos.); 700–2300 m; early June to early September.

Until fairly recently, only a few collections referable to *E. flexuosus* s. str. were available. Thus, their characteristic rosettes of basal leaves (1–3-nerved) and their habital similarity to *E. lassenianus* were not evident. Hairs on the stems of some plants, especially those from Trinity Co., are only weakly spreading, unlike those of typical *E. lassenianus*. In number of heads per stem, numbers and sizes of phyllaries and florets, and glandular hairs of the phyllaries, however, these plants correspond very well with typical *E. lassenianus*. Consequently, we choose to treat the two as one.

Note: Plants from Mendocino Co. (all from near Hell's Half Acre north of Hull Mt.) have phyllaries eglandular or nearly so and in this regard are similar to *E. eatonii* var. *plantagineus*. Plants with sparsely glandular phyllaries and hairs of the stems spreading to appressed are found near Red Clover Valley, Plumas Co., e.g., *A. A. Heller 8704* and *J. L. Strother 1360*. In *Strother 1360*, $2n = 9$ II with regular meiosis. Although these collections are somewhat atypical and approach *E. eatonii* var. *plantagineus* (q.v.), we include them here in *E. lassenianus*.

5. *ERIGERON NEVADINCOLA* S. F. Blake, Proc. Biol. Soc. Wash. 35: 78. 1922.—*Erigeron nevadense* A. Gray, Proc. Amer. Acad. Arts 8:649. 1873, non Wedd. 1857.—LECTOTYPE (Cronquist 1947): Nevada, Storey Co., “Cedar Hill and Mt. Davidson, near Virginia City” (label), 1863–64, *H. G. Bloomer s.n.* (Lectotype: GH!).

Stems decumbent to erect, 14–22(–33) mm long, usually green or stramineous at base, sparsely to moderately appressed-strigillose (sometimes with patent hairs, see discussion), the hairs 0.2–0.7 mm long; basal leaves linear to oblanceolate or spatulate, the longest 6–12(–19) cm long, 3–6(–13) mm wide; mid-stem leaves linear to narrowly oblong, 2–4(–7) cm long, 1–3(–7) mm wide, often with wavy margins; all leaves sparsely to moderately pilo-hirtellous to ascending-strigillose, sometimes minutely glandular as well; flowering stems bearing 1 head (rarely 2), heads held well beyond the basal leaves at peak anthesis, stem/basal-leaf length = 1.5–3.3; involucre broadly hemispheric to turbinate, (14–)17–23 mm diam. (pressed); phyl-

laries 31–68, weakly graduate, linear to lanceolate, length 4.7–6.6 times width, the longest 7–10.5 mm long, villous with hairs 1–2 mm long, little if at all glandular; ray florets 22–39, corollas white, often flushed with pale lavender or pink on abaxial (sometimes adaxial) face, rarely suffused with lavender, lamina 7–11 mm long, 1.5–3 mm wide; disc florets 150–250+, corollas ochroleucous or yellowish, 4.4–6.8 mm long; achenes stramineous to whitish with pale or orange ribs, 4–4.5 mm long, strigo-hirtellous to subsericeous; pappus of 20–24+ stramineous, rather coarse, barbellate bristles 4–5 mm long plus 12–20 setae 0.3–1 mm long.

Meadowy places and gravelly slopes, mostly in sagebrush and pinyon-juniper communities; northeastern to west-central Nevada (Elko, Humboldt, Lander, Lyon, Ormsby, Pershing, Storey, and Washoe cos.) and adjacent California (Lassen and Sierra cos.); 1450–2850 m; mid-May to late July.

Occasional plants (e.g., *Schoolcraft* 984 from east of Skedaddle Creek, Washoe Co., NV) are intermediate between *E. nevadincola* and *E. eatonii* var. *plantagineus*. Populations from the Virginia Range, Lyon Co., NV (e.g., *Tiehm* 7728 and 7814) that match typical *E. nevadincola* in most traits include some plants with typical, appressed-strigillose indument on stems and other plants with strongly spreading to quite erect hairs on stems. This dimorphism is also encountered in *E. eatonii* var. *eatonii* (q.v.).

6. ERIGERON SONNEI E. Greene, Pittonia 1:218. 1888.—*Erigeron nevadensis* (sic) A. Gray var. *sonnei* (E. Greene) Smiley, Univ. Calif. Publ. Bot. 9:373. 1921.—TYPE: protologue: “Western slope of the Washoe Mountains, Nevada”; label: “Nevada and Placer Counties, Cal., W. slope Washoe Mts.”, 22 Jul 1888, C. F. Sonne “2” (Holotype: ND-G!).

Stems prostrate to decumbent or erect, 4–12(–21) cm long, stramineous or somewhat reddish at base, sparsely to moderately strigillose with appressed or ascending hairs 0.1–0.7 mm long, not glandular; basal leaves linear to narrowly oblanceolate, the longest 3–10 cm long, (1.5–)4–6 mm wide; mid-stem leaves linear, 1–3 cm long, (0.7–)2–4 mm wide; all leaves sparsely to moderately pilohirtellous to ascending-strigillose, not glandular; flowering stems bearing 1 head (rarely 2), the heads held just beyond to well beyond the basal leaves at peak anthesis, stem/basal-leaf length = 1.2–3; involucre broadly hemispheric to subrotate, (8–)12–16 mm diam. (pressed); phyllaries 22–50, subequal or weakly graduate, linear to lanceolate, length 3.8–5.5 times width, the longest 4.5–8 mm long, flat to weakly navicular, noticeably scarious-margined, hirsutulous to villous with hairs 0.5–1.5 mm long, not glandular; ray florets 15–36, corollas white, usually flushed abaxially with pink, lavender, or violet, lamina 4.5–6.6(–8.5) mm long, 1.5–2.5 mm wide; disc florets 80–150+, corollas ochroleucous to yellow, sometimes tipped with

red, 3.5–5 mm long; achenes tan to reddish brown with stramineous to orange ribs, 2.8–3.5 mm long, strigo-hirtellous, more so distally; pappus of 18–30 barbellate bristles 3.5–5 mm long plus 8–12 fine setae 0.5–1.5 mm long; $2n = 18$ (determined from *Strother 1357*, CA, Alpine Co.).

Meadowy places, seeps, or rocky flats, often with sagebrush; California (Alpine, Eldorado, Mono, Nevada, Placer?, Plumas?, and Sierra cos.) and Nevada (Lyon, Nye, and Washoe cos.); 1800–2800 m; late May to early September.

Many specimens from along the border of California and Nevada near Lake Tahoe cannot be assigned confidently to either *E. sonnei* or *E. nevadincola*; elsewhere the two morphs are easily distinguished. These intergrading taxa are probably conspecific; we maintain them at specific rank for the present in order to preserve established nomenclature. Some plants from north of Lake Tahoe (e.g., old Lemon collections labeled “Sierra Valley”) are intermediate between *E. sonnei* and *E. eatonii* var. *plantagineus*.

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A COMPARISON OF NORTH AND SOUTH AMERICAN *LUPINUS* GROUP *MICROCARPI* (LEGUMINOSAE)

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ABSTRACT

Lupinus group *Microcarpi* occurs disjunctly in North and South America, primarily in central California and Chile. This study addresses the question of whether the disjunct representatives, variously referred to *L. microcarpus*, *L. densiflorus*, *L. ruber* or *L. subvexus*, are distinct. Data for vegetative and floral features were taken from South American specimens and were compared to those from population samples from California. The analyses show that some South American plants are smaller, but in all features have a range of variation within that of California plants. Affinities of the South American specimens were assessed by multigroup discriminant analysis and an a posteriori classification procedure whereby each one was assigned to a population sample from California. The South American specimens were assigned to a few California populations identified as *L. densiflorus*, *L. subvexus* and *L. ruber*, or intermediates between them. Neither floral nor vegetative features can be used to distinguish the South American representatives of group *Microcarpi* from some North American representatives.

RESUMEN

Lupinus del grupo *Microcarpi* ocurre descontinuadamente en América del Norte y del Sur, principalmente en California Central y en Chile. Este estudio se dirige a tratar de resolver la pregunta que si las especies llamadas *L. microcarpus*, *L. densiflorus*, *L. ruber* y *L. subvexus* son distintas. Los datos de las características vegetativas y florales fueron tomados de ejemplares sudamericanos y comparados con ejemplares obtenidos de poblaciones en California. El análisis de los datos indica que algunas de las plantas sudamericanas son más pequeñas que las de California, pero en todas las otras características, el rango de variación está dentro del que se obtiene de los ejemplares obtenidos en California. Las afinidades de los ejemplares sudamericanos fueron valorados por medio de un análisis discriminativo multigrupo y un método de clasificación de posterioridad en el cual cada uno de los ejemplares sudamericanos fueron asignados a una muestra de la población de California. Los ejemplares sudamericanos se asignaron a unas poblaciones californianas identificadas como *L. densiflorus*, *L. ruber* y *L. subvexus* o especies intermedias. Las características vegetativas y florales no se pueden usar para distinguir entre las especies obtenidas en América del Sur y aquellas obtenidas en California.

The informal group *Microcarpi* is easily delimited from the various assemblages of *Lupinus* summarized by Charles Piper Smith (1944). It is a group of annuals with sessile perfoliate cotyledons, ovoid two-seeded fruits and verticillate flowers. Members of the group occur disjunctly in North and South America, primarily in central California and Chile.

In a series of papers Smith (1917, 1918a,b, 1919) treated the *Microcarpi* as consisting of five species including 35 new or newly combined varieties. The group has not been studied in its entirety since. Authors of regional floras have treated it only in part, and their various interpretations largely have resulted in a more confusing taxonomy. No two subsequent treatments are in complete agreement as to the disposition of the taxa or the names to be used for them. The disagreement centers around a fundamental taxonomic question: are populations from North and South America distinct?

In this paper I compare morphological data obtained from herbarium specimens from South America with those obtained from population samples from California. The aim of the comparison is to document the range of morphological variation in the disjunct representatives, and to determine if the South American plants are morphologically distinct from their North American counterparts. I also compare distributional and ecological information obtained from the specimens and from my collection data.

HISTORICAL PERSPECTIVE

Smith's (1917, 1918a,b, 1919) group *Microcarpi* included *L. microcarpus* Sims, described from plants grown from seed originally collected in Chile, and *L. densiflorus* Benth., described from plants grown from seed collected by Douglas in California. Smith also recognized *L. subvexus* C. P. Smith, *L. horizontalis* Heller and *L. luteolus* Kell. Three of these (*L. microcarpus*, *L. densiflorus* and *L. subvexus*) were described as occurring in both North and South America. These three and *L. horizontalis*, of California desert habitats (Smith 1918a), form a problematical complex. The fifth species, *L. luteolus*, was described as occurring in California and Oregon. It can be separated from the complex by several features (Smith 1919a), and has been treated as a distinct species by subsequent authors.

Jepson (1936) commented on the close resemblance of North and South American specimens. He wrote (p. 278), "In certain cases, if the labels were removed, it would seem impossible, on the basis of the material itself, to say whether a given sheet were Californian or Chilean." Jepson placed all California representatives of the complex into *L. microcarpus*. He considered a portion of the California material, including *L. subvexus*, to be typical of the species. He recognized three additional varieties, *L. m.* var. *densiflorus* Jeps., *L. m.* var. *horizontalis* Jeps., and *L. m.* var. *ruber* (Heller) C. P. Smith (= *L. ruber* Heller).

The only other work in which North American members of the complex are treated as *L. microcarpus* is that of Hitchcock et al. (1961). They recognized *L. m.* var. *scopulorum* C. P. Smith from

Vancouver Island and adjacent islands of Washington, and *L. m.* var. *microcarpus* for all other populations from Washington to Baja California, and South America.

Munz's (1959) treatment of the California complex is diametrically opposed to Jepson's. Munz recognized *L. horizontalis*, *L. ruber*, *L. subvexus* with four varieties, and *L. densiflorus* with six varieties. From this treatment it might be concluded that the name, *L. microcarpus*, does not apply to North American plants.

Dunn and Gillett (1966) stated that *L. microcarpus* is a southern hemisphere relative of the *L. densiflorus* complex of the northern hemisphere. They concluded that North American taxa could not be interpreted as *L. microcarpus* because its original description referred to blue flowers and torulose pods, but did not refer to keel ciliation.

In a recent dissertation Planchuelo (1978) placed all Argentinean specimens of the group into *L. microcarpus*. She treated the Argentinean taxa described by Smith (1943) as synonyms, but did not study the Chilean taxa described by Smith (1918a,b, 1940).

To avoid confusion in the following discussion, I refer to North American representatives as the *L. densiflorus* complex, and follow Munz's (1959) treatment. *Lupinus luteolus* is excluded from the study.

METHODS AND MATERIALS

To document geographic distribution of South American members of group *Microcarpi*, I examined approximately 125 collections from BM, CAS, DS, GH, K, MO, RSA, UC and US. Collection data for those used in the analyses are given in Table 1. A total of 74 specimens for 56 collections were measured, and are identified by numbers as given in Table 1. The South American specimens include representatives of the nine taxa recognized by Smith (1918a,b, 1940, 1943) as occurring in Chile and Argentina. Six collections are type specimens.

To document distribution and variation of North American taxa, I collected extensively in California and consulted herbarium specimens from outside the state. The 41 samples used here (Table 2) are part of a larger study of the *L. densiflorus* complex in California. Each sample consisted of 20 plants, so data from 820 specimens form the data base. Most of the samples are from San Luis Obispo Co., near the center of the range of the complex and where all four species (*L. densiflorus*, *L. ruber*, *L. subvexus*, *L. horizontalis*) are known to occur (Munz 1959, Hoover 1970). The populations are from localities along west to east climatic gradients characterized by decreasing winter rainfall and increasing summer temperatures. Although the majority of populations can be identified as belonging

TABLE 1. COLLECTION DATA FOR SOUTH AMERICAN SPECIMENS OF *Lupinus*. Numbers in parentheses represent identification numbers for purposes of analysis. An asterisk (*) designates specimens for which data for all variables were obtained and included in the diagnosis.

Without collection data (1 GH*). Argentina, Chubut: Pampette s. of Lago Colhué Huapi, Riggs 56 (type of *L. verticillatus* C. P. Smith, 2 GH*). Neuquen: Chos Malal y Agrio, 600–1200 m, Comber 188 (type of *L. comberanus* C. P. Smith, 3 K*). Río Negro: Vicinity of General Roca, 250–360 m, Fischer 280 (type of *L. fischerianus* C. P. Smith, 4 BM, GH*, K). Chile, without collection data (5 BM*); without locality, Cumming s.n. (6 BM*); Cumming 567 (7 BM); Cruckshanks 135 (8 K*); 1832, Bridges s.n. (9 K*); 1864–65, Reed s.n. (10a, b K* 2 sheets); Feb 1888, Philippi s.n. (11 K*). Province undetermined, Andes, Reynolds s.n. (12 GH*); Salto de Conchalí, Nov 1883, Philippi s.n. (13 BM*); San Pedro Nolasco, collector unknown (14 BM*); Cordillero de Curico, Ruiz P. s.n. (15 GH*). Aconcagua: Uspallata Pass, Juncal, 2300 m, Buchtien 1180 (16a BM*, 16b GH*). Antofagasta: Taltal, 600 m, Werderman 856 (17a BM*, 17b DS*, 17c GH*, 17d K*, 17e UC*); ca. 10 km e. of Taltal, 75 m, Worth and Morrison 15807 (18 UC). Arauco: Arauco, Pennell 1297 (19 GH*). Atacama: Cerro Campaña, 15 Nov 1884, Philippi and Borchers s.n. (20 BM); Río San-carrón below Rucas, ca. 3200 m, Johnston 6204 (21a GH*, 21b K*). Biobío: Pailahueque, Pirion 203 (22 GH*). Cautín: Between Temuco and Río Quepe, Dec 1905, collector unknown (23 BM*); Temuco, Elliott 218 (24 BM*). Colchagua: San Fernando near Tinguiririca Bridge, Montero 15 (25 GH*). Coquimbo: Baños del Toro, 3500 m, Werdermann 197 (26a BM*, 26b CAS*, 26c GH*, 26d UC*); Coquimbo, July–Aug 1856, Harvey s.n. (27 GH*, K); 14 km e. of Nueva Elqui, 3200 m, Wagenknecht 18122 (28 GH*, UC). Concepción: Concepción, Reed s.n. (type of *L. densiflorus* var. *reedii* C. P. Smith, 29 GH*); Concepción, Elliott 78 (30 BM*); Concepción, Nov 1926, Günther and Buchtien s.n. (31 BM*); Lota, 7 Nov 1868, Cunningham s.n. (32 K*); Lota, 20 Dec 1902, Elwes s.n. (33 K*). O'Higgins: Rancagua, Bertero s.n. (34 K*); Cachapual, Rancagua, Bertero 393 (35 GH*); Cachapual, Rancagua, Bertero 393 et 1116 (36a BM*, 36b GH*). Santiago: Bath of Colina, 1825, Macrae s.n. (type of *L. densiflorus* var. *barbatissimus* C. P. Smith, 37 GH*, K); Colina, 1825, Macrae s.n. (38 K*); 3 km n. of El Tabo, 20 m, 30 Nov 1970, Simon s.n. (39 DS*, RSA); Río Teso Romeral, Biere 57 (40 GH*). Talca: Talca, Nov 1925, Gunkel s.n. (41 GH*). Valparaíso: Valparaíso, Cumming 567 (42a BM*, 42b K*); Valparaíso, 1844, Bridges s.n. (43 BM*); rd from Valparaíso to Quillota, Bridges s.n. (type of *L. densiflorus* var. *decumbens* C. P. Smith, 44 K*); Valparaíso, Cumming s.n. (45 K*); Valparaíso, Robinson s.n. (46 K*); Valparaíso, Mathews 363 (47a BM*, 47b GH*, 47c K*); Valparaíso, 1914, Calvert s.n. (48 BM); ca. 4 km from Valparaíso on rd to Quebrada Verde, 290 m, Morrison 16713 (49a GH*, 49b K*, UC); Renaca ca. 18 km from Valparaíso, 10 m, Morrison 16847 (50 GH*, K, UC); between Viña del Mar and Concón, 60 m, Landeman 193 (51a BM*, 51b K*); Viña del Mar a Concón, Pirion 268 (52 GH*); Concón, collector unknown (53 BM*); 21 m wege nach Concón, Nov 1928, Günther and Buchtien s.n. (54a CAS*, 54b DS*); 6.2 km n. of Puchuncavía, 30 m, Simon 134 (55 CAS*, RSA); Limache, Camino al Pugal, Looser 135 (56 GH*).

to one of the four species of Munz and Hoover, several are morphologically intermediate and cannot be identified with certainty.

Morphological data consisted of seven vegetative and 12 floral variables. Leaf measurements were taken from the largest leaf of the specimen, and floral measurements from flowers at anthesis. Seventeen quantitative variables are listed in Table 3. The other two

TABLE 2. COLLECTION DATA FOR CALIFORNIA POPULATION SAMPLES OF THE *Lupinus densiflorus* COMPLEX. Collection numbers are those of the author.

<p>Kern Co.: 1.0 mi n. of Reyes Sta., 1134; Crocker Cyn., 2.9 mi e. of San Luis Obispo Co. line, 1154; Gypsum Mine Rd., 1.0 mi e. of Simmler-Bitterwater Rd., 1186. Monterey Co.: county rd G19, 1 mi w. of US 101, n. of Bradley, 1179. San Luis Obispo Co.: CA 166, 3.1 mi w. of Sierra Madre Rd., 1133; county rd 285, 0.9 mi se. of CA 58, 1137; Hurricane Rd., 0.9 mi ne. of county rd 285, 1138; base of Crocker Grade at county rd 285, 1139; 1140; slope w. of San Juan R. at CA 58, 1141; Shell Cr. Rd. at CA 58, 1142; Atascadero-Creston Rd., 1.9 mi e. of Templeton Rd., 1143; Huerhuero-LaPanza Rd., 0.2 mi nw. of CA 58, 1144; CA 41, 0.7 mi e. of Cripple Cr. Rd., 1145; El Camino Real, Santa Margarita, 0.3 mi e. of US 101, 1146; Pozo Rd., 0.3 mi e. of CA 58, 1147; Pozo Rd., 0.7 mi w. of Salinas R. Bridge, 1148; CA 166, 11.9 mi e. of US 101, 1149; CA 166, 3.2 mi e. of Sierra Madre Rd., 1150; Hi Mt. Rd., 8.8 mi ne. of Lopez Lake Rd., 1151; Klau Mine Rd. just e. of Cypress Mt. Rd., 1152; county rd 285, 6.9 mi s. of CA 58, 1153; Elkhorn Trail Rd., 4.8 mi se. of Hurricane Rd., 1155; 1156; county rd 285, 2.3 mi n. of Coachoro Camp Rd., 1157; 1158; Avenales Ranch Rd., 3.3 mi e. of American Cyn. Rd., 1160; Avenales Ranch Rd., 0.3 mi ne. of Avenales Guard Sta., 1161; Avenales Ranch Rd., 2.0 mi se. of Avenales Guard Sta., 1162; 1163; USFS Rd., 2.1 mi e. of Los Machos Cr., 1171; 1172; Thirty-Five Cyn. Rd., 2.7 mi s. of Branch Mt. Rd., 1173; Cable Corral Rd. at CA 166, 1174; Almond Spring Ranch, Adelaida-Nacimiento Rd., 1175; Nacimiento Rd., 1.4 mi e. Chimney Rock Rd., 1176; Nacimiento Lake Rd., 0.6 mi n. of Nacimiento Dam, 1177; Wellsona Rd. at River Rd., 1180; El Pomar Rd., 0.1 mi s. of Vaquero Drive, 1181; Eagle Ranch, 0.3 mi s. of Santa Barbara Rd. n. of Santa Margarita, 1182; Camatti Cyn. Rd., 1.2 mi s. of Gillis Cyn. Rd., 1185.</p>
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were appraisals of wing and keel ciliation. Wing ciliation was recorded as either of three states: 0, absent; 1, present above; 2, present above and below. Keel ciliation was recorded as either of two states: 0, absent below; 1, present below. I selected the 19 variables to summarize size and shape of vegetative and floral structures, and to include features used in previous treatments.

Some taxonomic or field characters are not easily assessed for numerical analyses and were excluded for this reason. Smith (1918b et seq.), Munz (1959) and Hoover (1970) distinguished *L. densiflorus* as having spreading or arching racemes with secund flowers and fruits. This feature is related to the degree of branching on any one plant, and where the plants are growing. Often flowers on primary racemes do not become secund. Plants otherwise identifiable as *L. subvexus* or *L. horizontalis* may develop secund flowers and fruits. The feature is neither consistent within populations, nor unique to those identifiable by other features as *L. densiflorus*. Furthermore, it is extremely difficult to assess in pressed specimens if fruits are not present. *Lupinus horizontalis*, *L. ruber* and *L. subvexus* have been described as having ascending, erect or suberect flowers and fruits. Erectness is related to flower size; small flowers are ascending to erect whereas larger ones are suberect to spreading. The original figure of *L. microcarpus* showed ascending flowers, but the South

TABLE 3. RANGE AND MEAN VALUES FOR SOUTH AMERICAN AND CALIFORNIAN SPECIMENS OF *Lupinus* GROUP *Microcarpi*. All measures are in mm. n = number of specimens.

Variable	n	South American		Californian	
		Range	Mean	Range	Mean
Leaflet number	72	6-11	8.3	5-12	9.3
Leaflet width	71	2.0-12.0	5.1	2.0-12.5	6.9
Leaflet length	71	8.0-40.0	21.7	9.5-59.5	29.6
Petiole length	71	13.0-120.0	61.0	15.0-221.0	106.5
Peduncle length	72	15.0-150.0	65.7	19.0-320.0	140.1
Length between verticils 1 and 2	72	7.0-40.0	17.8	8.0-50.5	22.4
Bract length	72	2.5-8.5	5.0	3.5-12.5	6.3
Pedicle length	73	0.5-3.5	1.4	0.5-5.0	1.7
Upper calyx lobe length	73	2.2-5.0	3.7	1.1-7.8	4.0
Lower calyx lobe length	73	5.4-10.0	7.5	5.2-10.7	7.9
Banner length, base to flexion	74	4.5-8.0	5.8	4.2-10.6	6.8
Banner length, flexion to apex	74	4.5-8.2	5.7	3.7-9.7	6.5
Banner width, flexion to margin	74	1.4-3.5	2.5	1.3-6.2	3.5
Wing width	74	2.7-5.3	3.9	2.2-7.8	4.9
Wing length	74	9.0-14.4	11.7	8.8-17.7	13.6
Keel length	73	9.2-14.0	11.7	8.4-17.7	12.9
Keel width	73	0.9-1.5	1.1	0.9-2.9	1.7

American specimens exhibit as much variation in this feature as California plants.

Flower color in *L. densiflorus* varies from white to yellow, to pink and rose, and to lavender and purple. Often the amount of pink or purple varies in the wing and banner petals so that overall flower color is not easily described. Yellow and white flowers are generally restricted to populations of *L. densiflorus*, but all degrees of pink to purple are found in other members of the complex. Yellow, pink, and purple are generally intensified in dried specimens, but retention of original color is related to duration and method of drying. Sometimes flowers fade to a straw color on drying. The South American specimens do not appear to have flower colors different from California plants. Although the original description of *L. microcarpus* referred to blue flowers, all subsequent authors have described them as rose or lavender. I have not seen any specimen of the group that appears to have blue flowers typical of other lupine species.

Data analyses included a tabulation of minimum, maximum, and mean values for each variable. All variables could not be measured from some South American specimens, so the mean values were based on a varying number of observations (n) as given in Table 3. In addition, multigroup discriminant analysis and diagnosis were carried out as described in BIOSTAT II (Pimentel and Smith 1985). With these methods discriminant analysis is first performed on pop-

ulation samples, and then each individual of uncertain affinity is assigned to a population of the discriminant analysis by an a posteriori Geisser classification procedure. In this study discriminant analysis was performed on the samples from California, and the diagnosis on the South American specimens. Each South American specimen was assigned to a population sample from California. Because missing data are not allowed for these analyses, four South American collections (numbers 7, 18, 20 and 48) were excluded and the diagnosis was performed on 69 of the specimens indicated in Table 1. For these analyses the data were log transformed.

RESULTS

Geographic distribution. All South American specimens I examined are from Argentina and Chile. Smith's (1941) report of *L. microcarpus* from Peru was based on *Weberbauer 148* (Dpto. Lima, inter Matucana et Chanpothio, 26 Dec 1901, B) a specimen presumably destroyed.

Chilean plants occur along the coast from Taltal (25°26'S, Prov. Antofagasta) to Valdivia (39°49'S, Prov. Valdivia), and inland from Río Sancarrón (29°33'S, Prov. Atacama) to Temuco (38°44'S, Prov. Cautín). Approximately one-third of the specimens I examined were collected before 1900, many from areas near ports. Precise locality and habitat data are often scanty but are sufficient for the following ecological characterization. The Chilean plants grow in sandy soils, rocky places and grasslands from the coast to the Andes at elevations from near sea level to 600 m. A few specimens were collected along the western slope of the Andes at reported elevations of 2300 to 3500 m.

Argentinean plants occur from latitude 33°S in Prov. Mendoza to latitude 46°S near the southern border of Prov. Chubut. They grow in the same kinds of habitats as in Chile, but are regarded as rare and introduced (Planchuelo 1978).

In North America members of the *L. densiflorus* complex occur near the coast from San Diego Co. (32°N) to Humboldt Co., California (40–41°N), and disjunctly near Victoria, British Columbia (48°N). Inland localities extend from Sierra de Juarez, Baja California Norte (31°N) to central Washington (45°N). Within this range they are most abundant in California between latitudes 34°N and 38°N, from the coast eastward to the Sierra Nevada foothills. In central California these lupines grow primarily in sandy soils of valleys and low hills at elevations from near sea level to 1500 m. They are most abundant in roadside and intermittent streamside habitats, but also occur in grasslands and desert washes. They do not occur at elevations above 1550 m, nor east of the Sierra Nevada.

These distribution records, my field observations, and informa-

TABLE 4. ACTUAL AND PERCENTAGE OCCURRENCE OF WING AND KEEL CILIATION STATES IN SOUTH AMERICAN AND CALIFORNIAN SPECIMENS OF *Lupinus* GROUP *Microcarpi*.

	South American		Californian	
	n	%	n	%
Wing ciliation:				
0, absent	21	28	175	21
1, present above	46	67	539	66
2, present above and below	2	5	105	13
Keel ciliation:				
0, absent below	67	90	542	66
1, present below	7	10	277	34

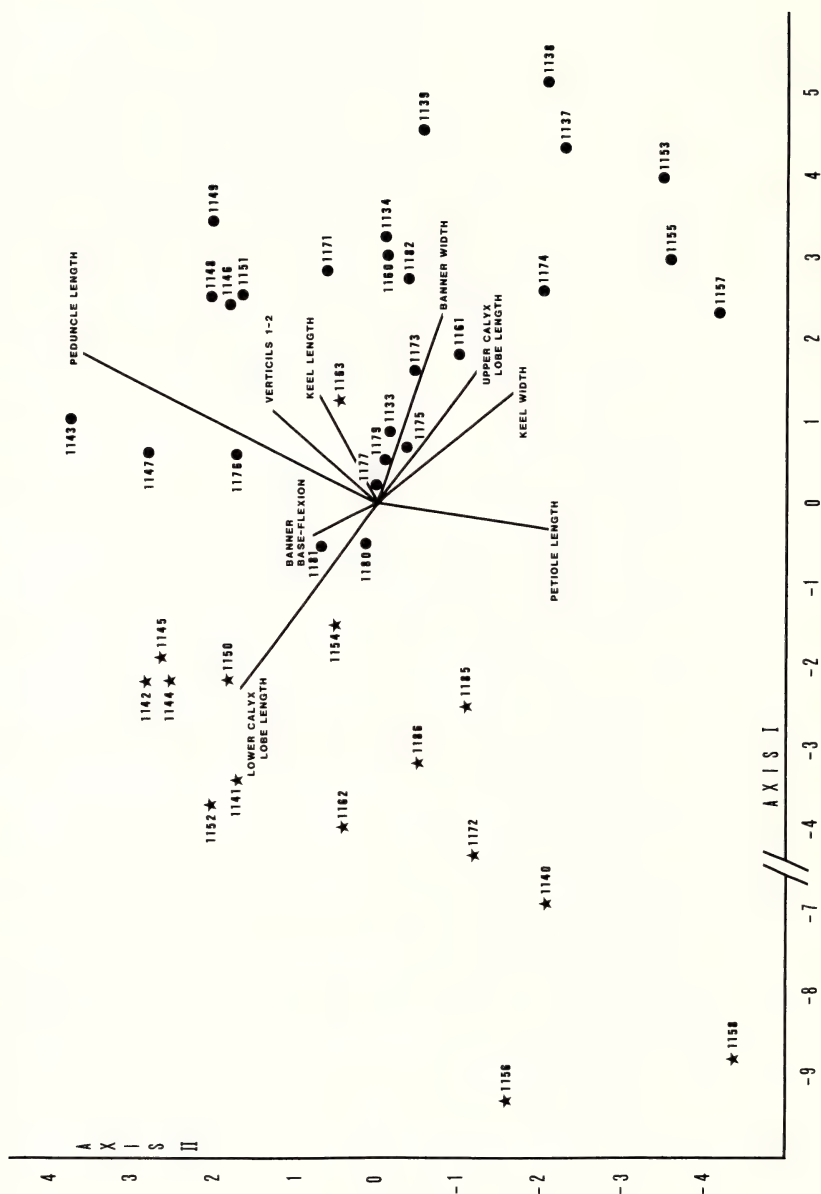
tion from the literature, indicate that plants from both hemispheres occur generally within the same latitudes and elevations, and in similar habitats. Both areas of distribution have Mediterranean climates and are well-known for their disjunct ranges of closely related species (Raven 1963).

Morphological comparisons. Table 3 shows that the South American specimens are often smaller, particularly in vegetative features, than the California specimens. South American specimens have a narrower range of variation than those from California, but generally exhibit a range of variation within that of the California specimens. Minimum values for five vegetative measurements were recorded from South American plants, but all maximum values were from California plants.

For all variables, South American specimens have smaller mean values than California specimens. Differences in mean values are particularly striking for the petiole and peduncle measurements. Differences in the mean values for the floral variables are less apparent. Except for wing and keel petal lengths, the differences between the two groups is ≤ 1 mm.

Results for wing and keel ciliation features are given in Table 4. Fewer South American specimens have cilia present on both margins of the wing and keel petals.

Although the aim of this paper is to determine if the South American representatives are distinct, some understanding of variation and discrimination of the California samples is necessary to clarify the relationships. Figure 1 portrays the results of the discriminant analysis of the California specimens on canonical axes 1 and 2 that respectively represent 47% and 16% of the differences between the samples. Vectors of variables contributing to ordination of the samples indicate that separation on axis 1 is primarily due to floral



variables, measurements of the calyx, and of the banner and keel petals. Samples on the right side of the graph have longer and wider keel petals, wider banner petals and longer upper calyx lobes than those on the left side of the graph. Separation on axis 2 is mostly due to vegetative features of peduncle, petiole and verticil lengths. Samples on the upper half of the graph are taller, whereas those on the lower half have smaller leaves. Ordination along axis two roughly parallels an east-to-west climatic gradient of arid-to-mesic habitats; samples on the lower half were collected in the most arid habitats.

Clear or tight clusters of the California samples are not detectable in Fig. 1. I initially identified the majority on the right side as *L. densiflorus*, and those on the lower right as *L. horizontalis*. The remote samples on the lower left were initially identified as *L. ruber*, and those on the upper left as *L. subvexus*. Several samples near the middle of the graph were identified as intermediate between *L. densiflorus* and *L. subvexus*, or intermediate between *L. subvexus* and *L. ruber*, and were collected in areas of sympatric distribution (Hoover 1970).

South American specimens were assigned to 15 samples designated by stars in Fig. 1. All except sample 1163 are on the left side of the graph, and are samples that were identified as *L. ruber*, *L. subvexus* or intermediates between them. Sample 1163 was initially identified as *L. densiflorus*. The 15 samples are from interior localities and more arid habitats than those not involved in the assignments.

Results of probability assignments for the South American specimens are summarized in Table 5. The probabilities ranged from 19% to 97% and averaged 51.4%. For 61 of 69 South American specimens, assignment to a specific California sample was evident; i.e., resemblance to any other sample was remote. Eight South American specimens (17c, 22, 26a, 31, 33, 36b, 38, 51b as identified in Table 1) had close affinities ($\leq 2\%$) to two different California samples; in each case the two samples were from nearby localities and like habitats. Forty (58%) of the South American specimens were assigned to just three California samples: 1142, 1162 and 1172.

The California samples show a clinal pattern of geographic variation (Fig. 1), but there is no evidence of a similar pattern among the South American specimens. This could be a reflection of inadequate sampling, although the specimens are from localities that represent the geographic range and ecological zones where they occur

←

FIG. 1. Plot of California samples of *Lupinus* group *Microcarpi* on canonical axes 1 and 2. South American specimens were assigned to those designated by stars. Vectors of variables contributing to the ordination are also plotted.

TABLE 5. DIAGNOSIS ASSIGNMENTS OF SOUTH AMERICAN SPECIMENS (S. Am.) TO CALIFORNIA (Calif.) POPULATION SAMPLES OF *Lupinus* GROUP *Microcarpi*. Column I refers to diagnosis based on 19 variables; Column II to that based on 17 variables.

S. Am.	Calif.			S. Am.	Calif.			S. Am.	Calif.		
	I	(%)	II		I	(%)	II		I	(%)	II
1	1162	(65)		21a	1158	(84)	1156	39	1186	(57)	
2	1172	(95)		21b	1158	(78)	1152	40	1150	(46)	
3	1185	(29)	1140	22	1163	(23)		41	1172	(36)	1162
4	1172	(54)		23	1154	(33)		42a	1141	(19)	
5	1154	(48)		24	1152	(36)		42b	1142	(57)	
6	1142	(26)	1150	25	1141	(54)		43	1142	(54)	1145
8	1156	(38)	1162	26a	1172	(51)		44	1162	(53)	1141
9	1162	(57)		26b	1140	(25)	1154	45	1142	(56)	1145
10a	1154	(31)	1145	26c	1162	(66)		46	1142	(49)	1145
10b	1156	(76)		26d	1172	(75)		47a	1142	(38)	1145
11	1150	(65)	1154	27	1162	(67)	1141	47b	1172	(63)	1145
12	1162	(55)		28	1162	(76)		47c	1172	(85)	
13	1162	(97)		29	1185	(43)	1186	49a	1172	(41)	1141
14	1162	(80)		30	1142	(66)		49b	1172	(79)	
15	1162	(34)		31	1145	(23)		50	1150	(58)	1145
16a	1162	(67)		32	1172	(69)		51a	1142	(42)	1145
16b	1156	(58)		33	1141	(37)		51b	1185	(21)	1141
17a	1158	(44)	1162	34	1142	(26)	1143	52	1150	(58)	
17b	1162	(35)	1141	35	1172	(52)	1145	53	1162	(57)	
17c	1158	(46)	1141	36a	1162	(84)		54a	1154	(27)	1150
17d	1172	(24)	1141	36b	1145	(23)		54b	1172	(48)	1141
17e	1172	(30)	1141	37	1144	(38)		55	1142	(80)	
19	1162	(87)		38	1145	(25)		56	1162	(80)	1141

in South America. Geographical variation among the South American plants would be detected by a differential affinity to the California plants; i.e., specimens would be assigned to populations from similar climatic and ecological zones in California. The South American specimens, however, were identified with a few samples from arid interior localities, the majority to three samples. Comparison of the 15 South American specimens assigned to sample 1172 illustrates that they are from localities of latitudinal and elevational extremes. They include specimen 2 from Prov. Chubut, Argentina at latitude 46°S, specimens 17d and 17e from Taltal, Chile at latitude 25°S, specimen 48 from Prov. Valparaiso, Chile at elevation 10 m, and specimens 26a and 26d from Prov. Coquimbo, Chile at elevation 3500 m. These results suggest that the South American plants exhibit a more mosaic pattern of variation than the California plants.

As shown in Table 3 South American specimens have shorter peduncles and petioles than California plants. Because these two variables were involved in the discriminant analysis (Fig. 1), assignment of the South American specimens could be influenced by the discrepant values. To test this hypothesis, a second diagnosis

was performed with these variables deleted. Assignment of 36 South American specimens was to the same sample as the previous analysis (Table 5). The assignments were to 14 samples, 13 in common with the previous diagnosis and an additional one (1143). There was some variation in the number of South American specimens assigned to the particular California samples, but the overall pattern of assignment did not change. These results show that the widely varying vegetative features do not influence the assignments of the South American specimens.

DISCUSSION AND CONCLUSIONS

Comparison of the disjunct representatives of *Lupinus* group *Microcarpi* reveals that vegetative structures are smaller in South American plants. As shown by the discrepant values for peduncle length, this size difference is ascribable to plant height. Two explanations can be advanced for the difference; one concerns environment and growing conditions, and the other collecting practices and sampling methodology.

Smith (1918a) pointed out that size and degree of branching of these lupines are a reflection of the plant's environment. Short, unbranched plants are generally found in arid habitats whereas tall, well-branched plants are generally found in more mesic environments. I have observed that plant size at any given locality can vary from year to year depending on relative amount and periodicity of precipitation and temperature extremes. The samples of California populations are from a variety of habitats and were made during favorable years, but collection of individual plants was by random sampling. There is no reason to assume that the South American specimens were collected from less favorable habitats or during less favorable years, but herbarium specimens must be viewed, in an analytical sense, as representing biased samples.

I think the small size of the South American specimens is most likely attributable to past collecting practices. The majority of specimens were collected before 1900, and several during early botanical expeditions to South America. It is reasonable to assume that early collectors were concerned with obtaining as many specimens as possible with limited equipment and facilities, and consequently collected mostly small individuals.

The comparison reveals only slight differences in floral features between North and South American plants. The range of variation observed in South American specimens is within that of the California samples, but the mean values of the South American plants are slightly smaller. The difference in mean values is attributable to relative abundance of large flowered *L. densiflorus* and *L. horizontalis* among the California samples. Fewer South American specimens have cilia present on both margins of the wing and keel petals.

These features are observed more frequently in *L. densiflorus* and *L. horizontalis*.

Although some South American specimens can be readily identified as *L. densiflorus*, the majority are more similar to California populations of *L. subvexus*, *L. ruber* or intermediates between them. The results clearly demonstrate that South American representatives of group *Microcarpi* are not distinct from some North American representatives. The implications of these results will be addressed in a forthcoming revision of group *Microcarpi*.

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LEPTODACTYLON PUNGENS SUBSP. *HAZELIAE*
(POLEMONIACEAE), A NEW COMBINATION FOR
A SNAKE RIVER CANYON ENDEMIC

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ABSTRACT

Morphological study of herbarium and living specimens of *Leptodactylon* from the Pacific Northwest and northern Great Basin indicates that the little-known species *Leptodactylon hazeliae* Peck is more appropriately treated as a subspecies of *L. pungens* (Torr.) Rydb. This rare taxon occurs only in the Snake River Canyon of Oregon and Idaho, where it inhabits sheer rock outcrops in *Poa-Agropyron-Purshia* communities. The relationship of subsp. *hazeliae* to other species of *Leptodactylon* is not clear. The subspecies is morphologically intermediate between *L. pungens* and *L. watsonii* (A. Gray) Greene, a trait it shares with the recently described *L. glabrum* Patterson and Yoder-Williams, an epilithic species of northern Nevada and adjacent Idaho. It is speculated that *L. glabrum* and subsp. *hazeliae* may have originated from past hybridization events involving *L. pungens* and *L. watsonii*.

Leptodactylon H. & A. is a small genus of suffrutescent perennials and low subshrubs endemic to western North America (Grant 1959, Cronquist 1984). It is primarily distributed in arid regions east of the Cascade-Sierran axis, but also occurs in the coastal mountains and maritime areas of southern California and adjacent Mexico. Its members are reminiscent of perennial species of *Phlox* and *Linnanthus*, but are distinguished from those genera by the combination of prickly leaves, prominent membranes in the calyx sinuses, and equally inserted stamens.

The generic limits of *Leptodactylon* are relatively well-marked morphologically, but the delineation of species and infraspecific taxa has been historically a source of frustration for students of Polemoniaceae. Several species exhibit considerable phenotypic plasticity, often with patterns of regional variation that are difficult to circumscribe. In the only comprehensive treatment of the genus, Wherry (1945) recognized 10 species and several varieties and formaes. Unfortunately, the relationships between morphology and geographic range presented in his account are vague, and the taxonomy has not been readily adaptable for use in state or local floras. Later workers (Davis 1950, Mason 1951, Harrington 1954, Cronquist 1959, 1984, Munz 1959, Kearney and Peebles 1960) reduced the number of accepted species to six or seven and elected to disregard

those proposed by Wherry (1945) that intergrade extensively across broad geographic zones. Some authors advocate the use of infra-specific categories to accommodate these variants. However, in lieu of detailed phytogeographic studies, the application of these names in any given area is largely conjectural.

Most of the variation in *Leptodactylon* is represented in a complex centered around *L. pungens* (Torr.) Rydb., one of three widespread, polymorphic species that range throughout all or much of the Intermountain Region and American Southwest. Fourteen of the twenty *Leptodactylon* taxa recognized by Wherry (1945) are segregates of *L. pungens*, and the species has a lengthy synonymy of over forty nomenclatural combinations dating to the early nineteenth century (Cronquist 1959, 1984). The other two intermountain species, *L. watsonii* (A. Gray) Greene and *L. caespitosum* Nutt., share a number of traits with *L. pungens*, and in some respects the three entities constitute a morphological continuum. Populations of the three species also overlap along an ecological gradient, and may coincide geographically, particularly in the eastern Great Basin and Wyoming. Despite the morphological similarities that imply common ancestry, and the high potential for sympatry, there are no available data to suggest that these species are interfertile. The two characters that typically are used to identify them, i.e., phyllotaxy and the number of flower parts, show remarkable consistency considering the overall variability of the groups. *Leptodactylon caespitosum* and *L. watsonii* are opposite-leaved and have 4-merous and 6-merous flowers, respectively, whereas *L. pungens* has 5-merous flowers and variable leaf insertion, usually with the upper alternate and the lower opposite. In the few cases where 5-merous flowers occur in *L. watsonii* (Cronquist 1984, Meinke pers. observ.), the plants are distinguished from the woodier *L. pungens* on the basis of flexible, subherbaceous flowering stems and opposite leaves throughout, including the inflorescence bracts.

Because of the consistency of the aforementioned differences, it is noteworthy that populations of *Leptodactylon* have been discovered recently that do not fit patterns of variation previously described for *L. pungens* or *L. watsonii*. The plants are located in the Snake River Canyon of northeastern Oregon and adjoining Idaho, a locality rich in disjunct and endemic species (Peck 1961). The most striking features of living specimens of the riverine populations are the short inflorescence branches, the pliable, bright green leaves, and the diurnal flowering that contrasts with the mostly vespertine corolla expansion of other Pacific Northwest *Leptodactylon* taxa.

My preliminary study showed that the plants correspond morphologically with the only known collection of *L. hazeliae* Peck, a taxon described in 1936 from three immature branches gathered

near the Snake River. Subsequent examination of several hundred herbarium specimens of *L. pungens* and *L. watsonii* supports the taxonomic recognition of the Snake River populations based on several minor but constant morphologic traits (Table 1). These plants are apparently ecologically specialized as well, being restricted to the uniquely mild (for the region) climate of the Snake River Canyon. The number of unambiguous characters separating the Snake River plants from other populations of *L. pungens* are fewer than the number distinguishing *L. pungens* from other species in the genus. I propose that these populations be recognized at the level of subspecies, under *L. pungens*. The spelling of the subspecific epithet in the following new combination reflects an orthographic correction from Peck's (1936) original "*Hazelae*", after Recommendation 73C.1b of the ICBN.

Leptodactylon pungens (Torr.) Rydb. subsp. ***hazeliae*** (Peck) Meinke, stat. et comb. nov. (Fig. 1)—*Leptodactylon Hazelae* Peck, Proc. Biol. Soc. Wash. 49:111. 1936; *L. pungens* subsp. *hookeri* (Dougl. ex Hook.) Wherry forma *hazelae* (Peck) Wherry, Amer. Midl. Naturalist 34:383. 1945.—TYPE: USA, OR, Wallowa Co., dry rocky slope, Snake River Canyon near mouth of Battle Creek, 13 Apr 1934, Barton s.n. (Holotype: WILLU 18415!).

Additional specimens. USA, ID, Idaho Co.: Snake River Canyon, ¼ mi downstream from Granite Creek, local on cliffs, 22 May 1974, Henderson, Wellner, and Bingham 1306 (ID!), two sheets); Snake River Canyon, Suicide Point, on trail near U.S. Forest Service sign, 15 Jun 1978, Mattson and Bishoff s.n. (IDF!). Adams Co.: Snake River Canyon, ca. 5 km s. of Hell's Canyon Dam, along Idaho Power Company right-of-way, 20 Apr 1977, Meinke 1545 (OSC!).

Habitat. *Leptodactylon pungens* subsp. *hazeliae* occurs below 650 m, inhabiting rock walls and talus covered slopes. It has only been recorded from the deepest part of the Snake River Canyon, between latitudes 45° and 46°N, and is not known to be sympatric with any other species or subspecies of *Leptodactylon*. The vegetation in this area is dominated by *Poa sandbergii* Vasey, *Agropyron spicatum* (Pursh) Scribn. & Smith, *Purshia tridentata* (Pursh) DC., and *Celtis reticulata* Torr. Other endemic taxa occurring with subsp. *hazeliae* include *Rubus bartonianus* Peck, *Ribes cereum* Dougl. var. *colubrinum* Hitchc., *Phlox colubrina* Wherry & Const., *Astragalus cusickii* Gray, *A. vallis* Jones, *Nemophila kirtleyi* Hend., and *Hackelia hispida* (Gray) Johnst.

Floral phenology. Branch development is initiated in late February or early March, with flowering occurring from April through June. Inflorescences consist of one to three flowers [not strictly single-

TABLE 1. MORPHOLOGICAL COMPARISON BETWEEN *Leptodactylon pungens* (EXCLUDING SUBSP. *hazeliae*), *L. pungens* SUBSP. *hazeliae*, AND *L. watsonii*.

Characteristic	<i>L. pungens</i>	<i>L. pungens</i> subsp. <i>hazeliae</i>	<i>L. watsonii</i>
Habit	Usually erect, flowering stems woody	Sprawling to mounded, flowering stems herbaceous	Sprawling or loosely matted, flowering stems herbaceous
Leaf insertion	All alternate, or lower opposite and upper alternate	Lower leaves alternate and upper opposite	Strictly opposite
Leaflets	1-1.8 mm broad, stiff, linear-lanceolate or subulate	0.2-0.6 mm broad, soft-filiform	0.8-1.2 mm broad, stiff, linear-lanceolate
Calyx	6-11 mm long, the lobes equal or nearly so	8-13 mm long, the lobes slightly unequal	8-14 mm long, the lobes markedly unequal
Number of perianth parts	5	5(-6)	(5)-6
Number of flowers per inflorescence	(3)-5-9(-15)	1-3(-5)	1-5(-9)
Stem, leaf, and calyx pubescence	Densely glandular-tomentose, pubescent, or glabrate	Finely stipitate-glandular	Glandular-pubescent or occasionally glabrate



FIG. 1. *Leptodactylon pungens* subsp. *hazeliae*. A. Flowering stem. B. Enlargement illustrating the glandular stem, leaf, and calyx pubescence.

flowered as reported by Peck (1936, 1961)]. Corollas generally remain open throughout the day and produce copious nectar. Insect visitors are primarily pierid and lycaenid butterflies and (occasionally) sphingid moths. Capsules are tardily dehiscent and persistent, with seed dispersal occurring throughout the summer.

Relationships. The taxonomic relationship between subsp. *hazeliae* and its potential relatives is difficult to assess. By tradition, the possession of pentamerous flowers and at least some clearly alternate leaves implies affiliation with *L. pungens*. However, the sprawling habit, herbaceous flowering stems, and sparsely flowered inflorescences are suggestive of *L. watsonii* (Table 1). Moreover, the presence of 5-merous flowers is not unprecedented in *L. watsonii*, being known from a few scattered localities such as the Quinn Canyon Range of central Nevada (Cronquist 1984). The habit and stem traits also are shared by *L. glabrum* Patterson and Yoder-Williams, a recently described species that occurs at two sites in northwestern Nevada and southwestern Idaho. *Leptodactylon glabrum* is considered closely allied with *L. watsonii* because of its completely opposite phyllotaxy and strictly 6-merous flowers (Patterson and Yoder-Williams 1984). It is possible that subsp. *hazeliae* has a close affinity with *L. glabrum* because it is the only other intermountain congener with soft, filiform-linear leaflets less than 0.5 mm broad. Furthermore, subsp. *hazeliae* plants also, on occasion, possess a few 6-merous flowers. Both entities are apparently restricted to rocky habitats isolated in steep canyons, and neither are known to be sympatric with other members of the *L. pungens* or *L. watsonii* complexes. Although leaf insertion and the number of flower parts will generally discriminate the two taxa, there are distinctive pubescence differences as well. *Leptodactylon glabrum* is eglandular and often glabrous (Patterson and Yoder-Williams 1984), whereas *L. pungens* subsp. *hazeliae* is stipitate-glandular on the stems, leaves, and calyces (Fig. 1B). Many of the morphological characters that distinguish *L. glabrum* and subsp. *hazeliae* within the genus are intermediate between *L. watsonii* and *L. pungens*. This, coupled with their narrow geographic distributions, suggests that the two endemics could be remnants of past intergradations between *L. watsonii* and *L. pungens* in areas where these widespread species no longer coexist.

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ANNOUNCEMENT

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SCUTELLARIA LUTILABIA (LABIATAE),
A NEW GYPSOPHILE FROM NUEVO LEÓN, MEXICO

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ABSTRACT

Scutellaria lutilabia, an endemic skullcap from an area of gypsum outcrops on the west side of Cerro Peña Nevada, Nuevo León, Mexico, is described. It appears to be a member of sect. *Resinosae* Epling but differs strongly from all species of that section by its vestiture, flower color, and mericarp morphology.

RESUMEN

Scutellaria lutilabia, una capa calavera de una afloramiento de rocas yesosas expuestas en el parte Oeste del Cerro Peña Nevada, Nuevo León, México, esta descrita. Parece ser un miembro de la secc. *Resinosae* Epling, pero se diferencia marcadamente de todos las especies de esa sección por su indumento, el color de sus flores, y su morfología mericarptica.

Intensive collecting on gypsum outcrops in northeastern Mexico has brought to attention a new species of *Scutellaria*.

***Scutellaria lutilabia* Lane & Nesom, sp. nov.**

Inter species sect. *Resinosae* Epling sed caulibus, foliis, pedicellis, et calycibus argenteo-virides cum pilis brevi-sericeis densis vestita. Corolla atosanguinea, labio inferiore cum macula lutea, et mericarpiis tuberculatis et brevi-aculeatis distingueda (Fig. 1).

Rounded to ascending, strongly taprooted, subshrubs 7–30 cm tall and to 70 cm wide, branched especially in the lower half; stems many, arising from an expanded and branched woody crown; stems, leaves, pedicels and calyces silver-green, densely clothed in a sericeous, antrorse vestiture of short, appressed white hairs to 0.25 (–0.5) mm long (Figs. 1–3); sessile glands present but obscured by the hairs. Leaves opposite, elliptic to ovate, 5–15 mm long, 3–7 mm wide, twice as long as wide, basally attenuate to a short petiole 1–2 mm on upper leaves and up to 5 mm on lower leaves, midrib and several pairs of lateral veins raised and prominent beneath, apex obtuse, margins slightly revolute, entire. Flowers solitary in axils, without subtending bracteoles; pedicels 2–4 mm long. Calyces

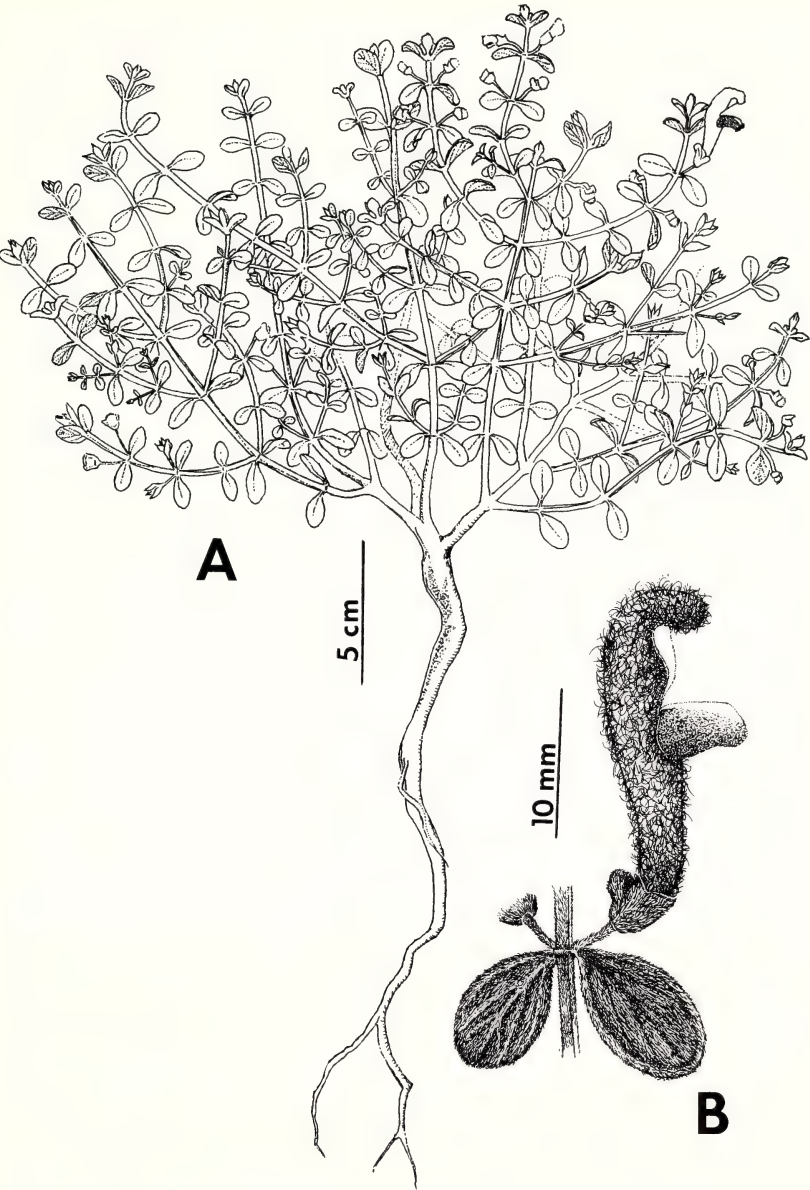


FIG. 1. *Scutellaria lutilabia*. A. Habit. B. Leaves, stem, and flower.

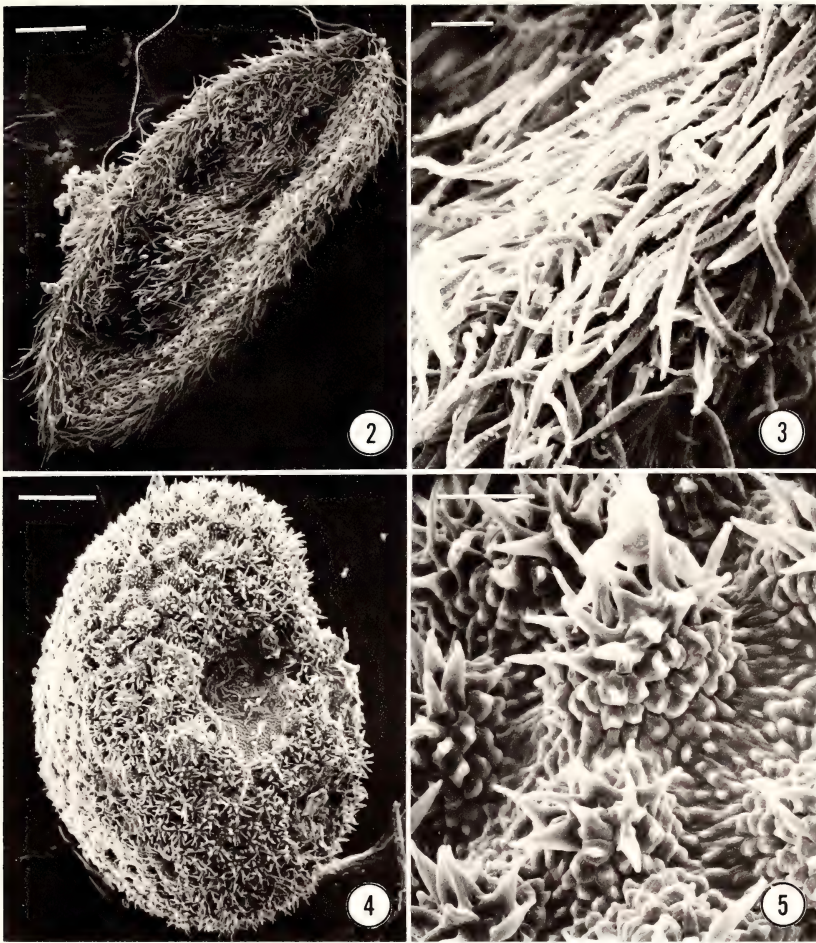
2-lipped, 4–5 mm long, accrescent and closing in fruit; upper lip expanded upwardly 3 mm into a dorsally impressed, shield-like scutellum and falling at maturity with the mericarps; lower lip dish-like, persistent. Corolla sigmoid in outline, 15–20 mm long, maroon, and densely villous on the outer surface with hairs to 1 mm long, bilabiate; lower lip 3-lobed, ca. 8 mm long and 8 mm wide with a median yellow-gold blotch starting just behind the tip and running into the throat; upper lip galeate, ca. 7 mm long, flaring and revolute at both axial edges, with some scattered villosity within; tube 10 mm long, ca. 2 mm wide, densely villous inside at base; stamens didynamous, included within the galea, basal anterior pair adnate ca. two-thirds their length and ultimately longer, basal posterior pair adnate ca. three-fourths their length; anthers maroon-purple, densely short-ciliate, with sessile glands along the line of attachment to the filament; gynoecium with an elevated 4-lobed ovary, free and gynobasic style, and a linear, 2-parted stigma inserted between the 2 anther pairs. Fruit (Figs. 4–5) 4 brownish-black, ovoid mericarps 1.5 mm long, 1 mm wide, surface with tubercles ca. $90 \times 90 \mu\text{m}$ with linear-lanceolate, outwardly elongated apical cells, giving the whole mericarp a densely and minutely hispidulous appearance.

TYPE: México, Nuevo León: ca. 30 km ene. of Doctor Arroyo, 21.5 km ene. of San Antonio de Peña Nevada, $23^{\circ}46'N$, $99^{\circ}55'W$, 2015 m, 3–5 Aug 1981 (fl, fr), *Nesom 4273* (Holotype: MEXU; isotypes: ARIZ, ASU, ENCB, NY, OS, US).

PARATYPES: México, Nuevo León: [type locality], 10 Jul 1984, *Michener 4428 with Prigge* (GH, to be distributed); ca. 7 km ne. of San Antonio de Peña Nevada, [1.3 km n. of the type locality], Jul 1977 (fl, fr), *Wells and Nesom 513* (LL, MO, NCU).

Habitat and distribution. *Scutellaria lutilabia* is known only from gypsum outcrops at an elevation of about 2000–2050 meters on the northwest slope and west base of Cerro Peña Nevada. It is associated there with *Agave*, *Bauhinia*, *Cowania*, *Euphorbia*, *Krameria*, *Leucophyllum*, *Lindleya*, *Mortonia*, *Nolina*, and *Opuntia*, as well as numerous herbaceous species.

Relationships. A suite of characteristics of the new species refer it to the southwestern U.S.-Mexican sect. *Resinosae* Epling (Epling 1942): a xeric habitat; a taproot topped by a woody crown from which arise numerous leafy stems; small, entire leaves; solitary flowers in the axils of the upper leaves; a broad, impressed scutellum; stamens attached near the center of the corolla tube; and mericarp epidermal cells generally with a circular outline at their bases (Fig. 5) (Lane 1983). Features that clearly separate this new species from other members of the section are its sericeous vestiture, densely “hispidulous” mericarps, and maroon corollas with a golden-yellow blotch on the lower corolla lip (from which the specific epithet is



FIGS. 2-5. *Scutellaria lutilabia*. 2. Young leaf. Note nature of vestiture, scale = 500 μm . 3. Detail of leaf vestiture, scale = 50 μm . 4. Mericarp lateral view, scale = 250 μm . 5. Detail of mericarp surface. Note elongated epidermal cells with hair-like extensions, scale = 50 μm . All from *Wells and Nesom 513*. Specimens processed via standard techniques (cf. Lane 1983).

derived). Other species of sect. *Resinosae* have more sparse or at least non-sericeous vestiture, tuberculate mericarps without apical extensions on the tuberculae, and blue or violet-blue corollas with a white blotch on the lower lip.

Scutellaria lutilabia stands apart morphologically from all other described taxa of sect. *Resinosae*. Perhaps its closest relative is an undescribed species from eastern Chihuahua (James Henrickson pers.

comm.), which is similar in habit (though more condensed and intricately branched), leaf morphology, and stem vestiture. In contrast, its flowers are blue with white markings and the mericarps are granular-papillate, lacking the prominent hispidulous surface of *S. lutilabia*. The papillae, however, are rough in appearance apparently because of unevenly protruding epidermal cells and need to be examined in closer detail for possible homologies with those of *S. lutilabia*.

Despite Epling's reservation about the taxonomic value of mericarp morphology, this character has been used previously in the delineation of species and species groups in *Scutellaria* (Lane 1983 and unpubl.). Many of Epling's groups display a high degree of homogeneity in the nature of their mericarp surface. Mericarp surfaces in American species of the genus have been described as smooth, roughened, rugose, granulate, squamellate, mammillate, lacerate-dentate angled, coarsely toothed, with peg-like processes, verrucose, muricate, tuberculate, lamellate, and papillate (see Epling 1942 and various floristic manuals). Epling described those of *S. horridula* Epling (sect. *Resinosae*) as "horridulis"; they have slender, strongly projecting tuberculae but lack the hairlike extensions as in *S. lutilabia*. Almost all of these descriptions, however, are based on observations made with only low magnification. We predict that SEM studies of mericarp surfaces will reveal similarities indicative of recent common ancestry.

ACKNOWLEDGMENTS

We are grateful to Maura McNulty for the illustrations, Stella Muller for the Spanish translation, and the first author thanks Laurie Stull for affording him writing time. SEM facilities were provided by the Department of Botany of the Ohio State University. James Henrickson made comments on the manuscript and generously provided information on undescribed species of *Scutellaria*. We thank David Michener and Barry Prigge for information on their recent collection.

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A NEW SPECIES OF *CROTON* (EUPHORBIACEAE) FROM NICARAGUA

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ABSTRACT

Croton nubigenus, a new species of cloud forests in northern Nicaragua, belongs to sect. *Tigium* and appears most closely related to Mexican species such as *C. adpersus*, *C. tremulifolius*, and *C. ynesae*, as well as *C. wilsonii* of Jamaica.

RESUMEN

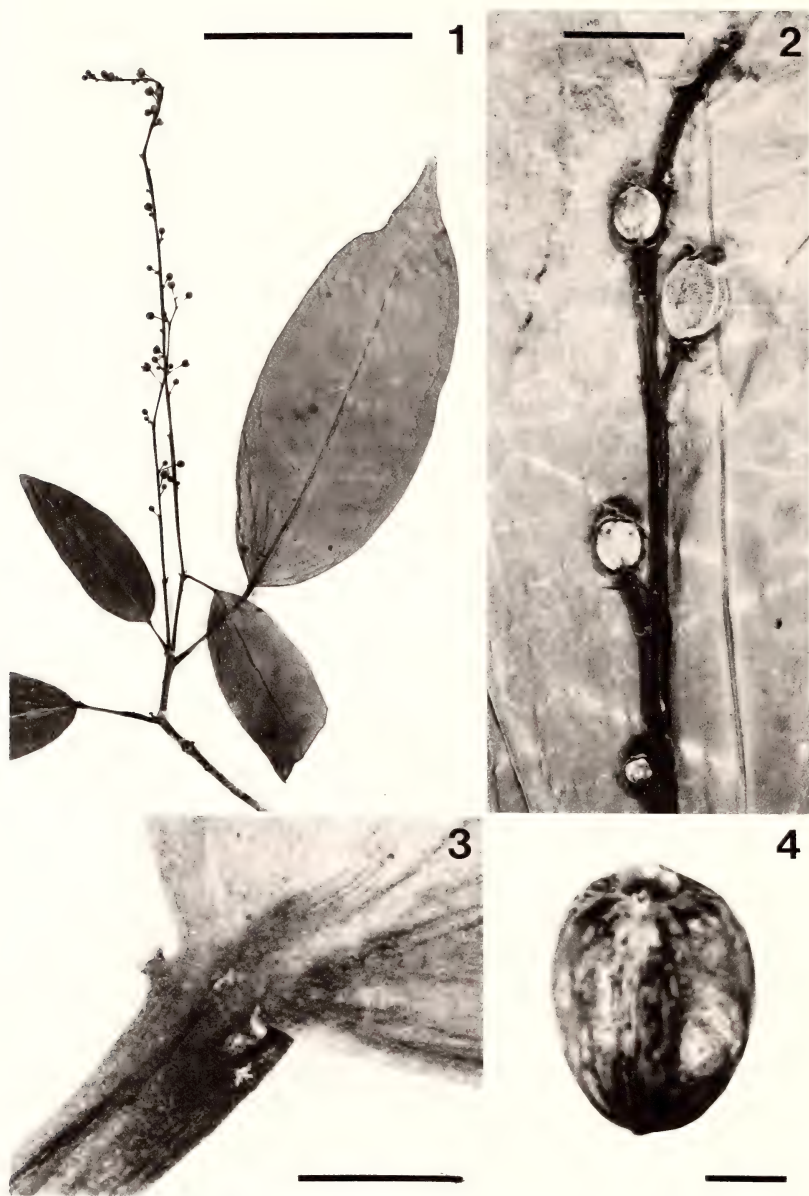
Croton nubigenus, una nueva especie de los bosques nublados del norte de Nicaragua, pertenece a la secc. *Tigium* y parece tener afinidades estrechas con algunas especies Mexicanas como *C. adpersus*, *C. tremulifolius*, y *C. ynesae*, incluyendo a *C. wilsonii* de Jamaica.

During the preparation of the treatment of the Euphorbiaceae for the "Flora of Nicaragua" project at the Missouri Botanical Garden, I encountered a number of specimens of a *Croton* from cloud forests on peaks in Nicaragua. These specimens represent a species not formerly described.

***Croton nubigenus* Webster, sp. nov. (Figs. 1–4)**

Arbor dioica, foliis penninerviis subglabris, limbo basi subsessilibiglanduloso, stipulis deltoidis, floribus receptaculo parce villosulo, staminibus 13–15, ovario stellato-hirtello, stylis bifidis, caruncula seminis obsoleta.

Dioecious shrubs or trees 3–5 m high; twigs and leaves nearly glabrous (with appressed pauciradiate stellate hairs mainly on flowers and young growth). Leaves with petioles 1.5–7 cm long; paired glands at apex of petiole subsessile, 0.4–0.6 mm high and broad; stipules deltate, 0.2–0.3 mm; blade chartaceous, oblong-lanceolate, bluntly acuminate at tip, cuneate at base, glabrous on both faces; venation pinnate, major lateral veins about 8–10 on a side, slightly arching, veinlet reticulum distinct but tenuous beneath; margins entire. Inflorescences terminal (and sometimes also at uppermost adjacent nodes), racemose, unisexual, 5–18 cm long; pistillate flowers solitary at nodes, 4–6 per raceme; staminate flowers 2–5 per node; bracts deltate, entire, about 0.5 mm long. Staminate flower: pedicel 2.5–4.5 mm long; sepals 5, valvate or slightly imbricate,



FIGS. 1-4. Photographs of *Croton nubigenus*. FIG. 1. Flowering branch of staminate plant (*Pipoly* 6038). FIG. 2. Apical portion of pistillate inflorescence (*Grijalva* 313). FIG. 3. Base of leaf blade showing petiolar glands (*Grijalva* 313). FIG. 4. Adaxial view of seed (*Pipoly* 6052). Bar equals 5 cm in Fig. 1, 1 cm in Fig. 2, 2.5 cm in Figs. 3 and 4.

deltate-ovate, acute, glabrous or with very sparse appressed stellate hairs, 1.8–2 mm long, 1.2–1.5 mm broad; receptacle sparsely villose; petals 5, elliptic-spatulate, glabrous on both faces, short-villosulous at tip and margins near base, 1.7–2 mm long, 0.5–0.8 mm broad; stamens 13–15; filaments glabrous, anthers 0.6–0.8 mm long. Pistillate flower: pedicel becoming 5–8.5 mm long, 0.8–1 mm thick, subglabrous; sepals 5, lanceolate, entire, acute, basally connate, 1.2–1.5 mm long, subglabrous or sparsely appressed-stellate abaxially, copiously hirsutulous (with simple hairs) adaxially; disk patelliform, thickish, shallowly 5-lobed, subglabrous, 1.5–1.8 mm across; petals obsolete (represented by tufted hairs); ovary ellipsoidal, densely stellate with more or less appressed 8–12-radiate hairs about 0.2–0.3 mm across; styles bifid, 2.5–3.5 mm long, branches slender. Capsule not seen intact; columella slender, 8–8.5 mm long; seeds plump, ellipsoidal, brownish, smooth, 7.3–8 mm long, 5.5–5.6 mm broad; caruncle reduced or obsolete.

TYPE: Nicaragua, Zelaya, primary cloud forest on summit of Cerro La Piminenta, 900–980 m, 13°45'N, 84°59'W, 13 Apr 1979, *Pipoly 5113* (Holotype: MO; isotype, DAV).

PARATYPES: Nicaragua, Zelaya, Cerro La Piminenta, *Pipoly 6038, 6052* (DAV, MO); Cerro El Hormiguero, *Grijalva 313, 462* (DAV, MO); Cano El Hormiguero, *Pipoly 6102* (DAV, MO).

This new species appears to be rather narrowly restricted to cloud forests on peaks of a small area of the Cordillera Isabella near the boundaries of the departments of Jinotega and Zelaya. In the last complete revision of *Croton* by Mueller Argovienensis (1866), it would key down near *Croton wilsonii* Griseb., a Jamaican species referred by Mueller to series III of sect. *Croton*. According to the revision of his supraspecific taxa of *Croton* in the “Flora Brasiliensis” (Mueller 1873), the position of *Croton wilsonii* would fall in sect. *Croton*, subsect. *Cleodora*, ser. *Medea*. As noted by Bentham (1880) and others, however, the sectional and subsectional taxa of Mueller are defined arbitrarily and often are highly unnatural. It appears on the basis of a number of common characters (discussed below) that *C. wilsonii* and *C. nubigenus* should be referred to sect. *Tigium* (Kl.) Baillon. Although Baillon (1858) included in his section the single species *C. tigium* L., a medicinal plant native to India, Mueller (1866) recognized several related Asiatic and African species (without, however, granting *Tigium* any formal taxonomic recognition).

In the absence of any thorough revision of the genus *Croton* during the century subsequent to Mueller’s monographic work, description of new species has taken place with little appreciation of possible biogeographic relationships. The relationships among species of sect. *Tigium* have been almost totally obscured by the complications of fragmentation of effort and failure of the classical 19th century classifications to adequately reflect phylogeny.

Croton nubigenus clearly belongs in the same section as *C. wilsonii* because of its sparse indumentum of appressed stellate hairs, penninerved leaves biglandular at base, small entire sepals of pistillate flowers and bifid styles. It differs from the Jamaican species, however, in its broader entire leaves, sexual condition (dioecious instead of monoecious), larger stamen number, and distinctly pedicellate pistillate flowers. Among species of mainland North America, *C. nubigenus* shows some similarity to *C. ynesae* Croizat from western Mexico. *Croton ynesae* nevertheless differs in many ways, including coarsely serrate leaves, monoecious inflorescences, reduced pistillate calyx, and carunculate seeds. In South America, there are a few species that are suggestively similar to *C. nubigenus*, including *C. fraseri* Muell. Arg. from Ecuador and *C. sapiifolius* Muell. Arg. from Brazil. Mueller (1865, 1866) made the latter species the type of sect. *Quadrilobus* Muell. Arg. because of the 4-merous flowers, but in both vegetative and floral characters it somewhat resembles *C. nubigenus* and *C. wilsonii*. If the American species of the "Tigium" alliance are treated as a section distinct from the Old World species, then sect. *Quadrilobus* would be the correct name. However, although our knowledge of these plants is still rather fragmentary, I believe that it is better to recognize sect. *Tigium* in an inclusive sense to include not only sect. *Quadrilobus* but also sect. *Gymnocroton* Baillon (1858), based on the Australian *C. verreauxii* Baillon. The widespread but fragmentary nature of the distribution of sect. *Tigium* (s. lat.) raises interesting biogeographical questions that can only be answered by a revision of the sections of *Croton*, and a more thorough study of the species putatively related to *C. nubigenus*.

ACKNOWLEDGMENTS

This new species of *Croton* was discovered during a winter interlude at the Missouri Botanical Garden, where studies were made in collaboration with the Flora of Nicaragua project, directed by Dr. W. Douglas Stevens. I wish to thank Ms. Lynn Gillespie for preparing the photographs.

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A NEW *LOMATIUM* (APIACEAE) FROM THE SIERRAN CREST OF CALIFORNIA

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ABSTRACT

Lomatium shevockii, a low, tufted, acaulescent species, is described from the southern Sierra Nevada, Kern County, California. Although the growth habit is reminiscent of some species of *Oreonana* and *Cymopterus*, the new species is clearly a *Lomatium*, based on morphology and ecology. It appears closely related to *Lomatium rigidum*, but differs strikingly by its flower color, subcapitate inflorescence, nearly prostrate peduncles, smaller leaves, and subsessile fruit.

An exceedingly rare species of *Lomatium* was discovered by Mr. Shevock on 7 April 1984 during a cursory field survey of Owens Peak via the newly constructed section of the Pacific Crest Trail north of Walker Pass. Although at that time only a few young leaves had emerged, the collector correctly identified the plants as "new" for the southern Sierra Nevada. At first glance the young leaves resemble those of *Oreonana clementis*. Closer observation of the blue-green, glabrous, white spinule-tipped leaves, however, resulted in a tentative assignment to *Cymopterus*—a genus that has several species with white-spinulose leaves. Subsequent collection of mature fruit in June 1986, conclusively placed the species in *Lomatium*.

***Lomatium shevockii* Hartman & Constance, sp. nov. (Fig. 1)**

Plantae perennes glabrae et glaucae acaulescentes 4–12 cm altae e radice palari elongato cum caudice fibrilloso. Folia rosulata ovato-deltaoidea 1.5–4 cm longa, 2–5 cm lata, 2–3-pinnato-pinnatifida divisionibus ultimis oblongis ovatisve saepe confluentibus acerosis; petioli 1.5–5.5 cm longis scarioso-vaginantibus. Pedunculi folia aequantes excedentesve 4–12 cm longi; involucrum plerumque nulum; radii 5–9 inaequales divergentes vel reflexi; umbellulae andromonoeciae ex floribus perfectis 5–10+ et floribus staminatis 1–4 constantes; involucellum dimidiatum bracteolis 3–6 lanceolatis vel ovatis integris distinctis 1–3.5 mm longis. Flores purpurei, sepalis

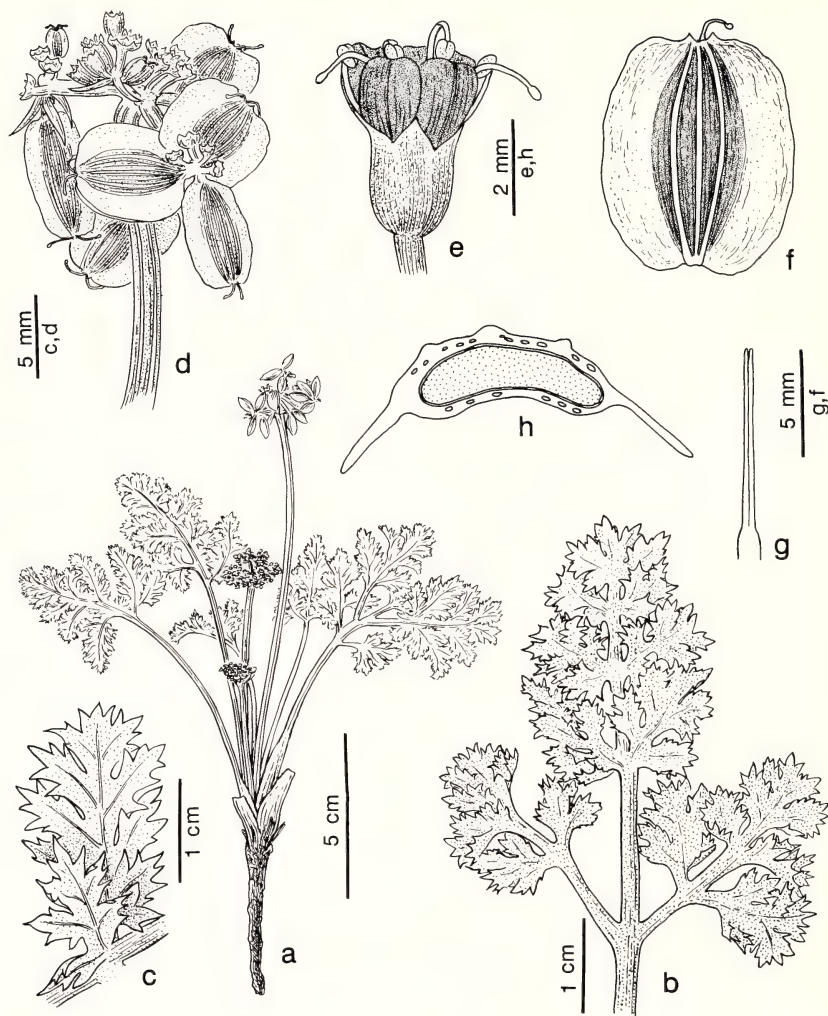


FIG. 1. *Lomatium shevockii*. a. Habit. b. Foliage leaf. c. Leaflet. d. Fruiting umbel. e. Flower. f. Fruit, dorsal view. g. Carpophore. h. Transverse section of mericarp. (a, c, e from Shevock et al. 11197; b, d, f-h from the type collection.)

evidentibus triangularibus vel lanceolatis, petalis obovatis, antheris flavis, stylis 2–2.5 mm longis; stylopodium nullum, disco praesenti; pedicelli usque ad 1 mm longi; carpophorum bipartitum. Fructus dorsaliter compressus ellipticus orbicularisve 8–10 mm longus 7–9 mm latus apice rotundatis basi emarginatis, alis tenuibus distinctis quam corpore parum angustioribus; vittae in intervallis 3–5, in commissuris 8–10.

Low, tufted, herbaceous perennial 4–12 cm tall, acaulescent, aromatic, with a primary root 20–30 cm long or more, 0.3–1.2 cm in diameter at summit, the crown unbranched or with few to several branches arising 4–15 cm below ground, the crown or branches enveloped their distal 1–3 cm by persistent leaf bases or their frayed remains, which may double the apparent diameter. Leaves broadly ovate to deltoid, 1.5–4 cm long, 2–5 cm wide, 2–3-pinnate-pinnatifid, pale green, glaucous, glabrous; primary leaf divisions 3–5 usually in opposite pairs, the terminal one deeply pinnate-1–2-pinnatifid, usually confluent with the upper pair, the lower distinct, more widely spread proximally, the lowest often remote, the lateral primary divisions asymmetrically pinnate-1–2-pinnatifid into 40–50 or more often confluent oblong to ovate segments, the lobes and teeth acrore; petiole subterete to grooved adaxially, 1.5–5.5 cm long, expanded at the base into a scarious sheath. Inflorescence a compact compound umbel 10–25 mm in diameter, or enlarging to 40 mm in fruit; peduncles ascending to erect in flower, or decumbent in fruit, 4–12 cm long, equaling to much exceeding the leaves, glabrous; involucre none, or rarely of an ovate to lanceolate bract 2–6 mm long; rays 5–9, 1–6 mm long in flower and up to 11 mm in fruit, subterete to flattened, unequal, those bearing fruit becoming divergent to reflexed and markedly enlarged at the base; umbellets andromonoecious, of 1–4 staminate and 5–10 (or more) perfect flowers or of all perfect or all staminate flowers; involucels dimidiate, of 3–6 mostly lanceolate to ovate bractlets that are entire, acute to acuminate, 1–3.5 mm long, and about equaling to somewhat exceeding the flowers, usually distinct or essentially so, with a thin, white or purplish, scarious margin, glabrous; pedicels 0.1–2 mm long on staminate flowers, 0.1–1 mm on hermaphroditic flowers, those bearing fruit becoming markedly enlarged at base. Flowers purple; sepals triangular to lanceolate, 0.2–0.6 mm long, often unequal, enlarging little in fruit, greenish; petals 1.6–1.9 mm long; anthers yellow, 0.7–0.8 mm long; filaments 1–1.3 mm long; styles subterete, 2–2.4 mm long, enlarging little in fruit, spreading to recurved; stylopodium none; disc present; ovary glabrous, glaucous; carpophore bipartite. Fruit dorsally flattened, broadly elliptic to orbicular, 8–10 mm long, 7–9 mm broad, glabrous, the wings distinct, narrower than the body; vittae 3–5 in intervals, 8–10 on commissure.

TYPE: CA, Kern Co., se. slope of Owens Peak, eastern crest of the southern Sierra Nevada, T25S R37E S21 ne.¼ MDB+M, 8200 ft (2500 m), 11 Jun 1986, *James R. Shevock 11681* (Holotype: UC; isotypes: CAS, MO, NY, RM, RSA, US).

PARATYPES: CA, Kern Co., type locality, 7 Apr 1984, *Shevock 10812* (CAS: leaf only), 27 May 1985, *Shevock, Norris & Rose 11197* (CAS, MO, NY, RM, RSA, UC); se. slope of Mt. Jenkins above Pacific Crest Trail, T25S R37E S34 nw.¼ MDB+M, 7300 ft (2225 m), 21 Apr 1986, *Shevock & Ertter 11439* (CAS, RSA, UC).

Distribution, ecology, and phenology. *Lomatium shevockii* occurs on colluvial slopes and talus, usually along contact zones of metamorphic and granitic rock in open mixed coniferous forest or pinyon pine/canyon live oak woodland. Populations are restricted to the eastern side of the crest, generally between 2225 and 2500 m. Plants occurring at the lower of these elevations are in canyon bottoms, where the seeds presumably washed downslope primarily from late summer thunderstorms. Flowers appear from late April to mid-May, with fruit developing by mid-June. All populations are on federal lands administered by the California Desert Conservation Area, Bureau of Land Management.

This *Lomatium* is apparently a very restricted endemic. Habitats with the combination of slope, aspect, geology, and elevation required by *L. shevockii* are limited along the rugged crest and are believed to comprise less than 5 air km. The population near the summit of Owens Peak is within an open, park-like mixed coniferous forest of *Pinus jeffreyi*, *P. flexilis*, *P. monophylla*, *P. lambertiana*, *Abies concolor*, and *Juniperus occidentalis* subsp. *australis*. On steeper slopes below this forest, the species extends into openings in the pinyon pine/canyon live oak woodland. The site of the small population on Mt. Jenkins lacks limber pines, but is otherwise similar. No single set of associated species accompany all populations of *Lomatium shevockii*, but *Allium burlewii*, *Eriogonum wrightii* var. *subscaposum*, *Mimulus* sp., *Monardella* spp., *Orochaenactis thysanocarpha*, *Salvia pachyphylla*, and *Zauschneria latifolia* were found in proximity.

Despite the rarity of the new species, the rugged terrain it inhabits should protect it from human disturbance. Other rare taxa being inventoried by the California Natural Diversity Data Base and the California Native Plant Society that are known to occur on Owens Peak include *Eriogonum breedlovei* var. *shevockii*, *Monardella* sp., *Phacelia novemmillensis*, and *Raillardella muiirii*.

Lomatium shevockii belongs to the *Euryptera* group, which comprises seven species and extends along the Pacific Coast from southern Oregon to Baja California and Guadalupe Island. Coulter and Rose (1900) said of *Euryptera*, which they treated as a genus distinct from *Lomatium*: "... differs from typical *Lomatium* especially in its foliage, which is much more simple, with broad often orbicular leaflets, and sharp mucronate teeth. The wings of the fruit are inclined to be distinct, while in *Lomatium* the wings are united and project below the seed."

ACKNOWLEDGMENTS

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ANNOUNCEMENT

NEW PUBLICATION

DORN, ROBERT D. 1988. *Vascular Plants of Wyoming*, illustrated by JANE L. DORN. Mountain West Publishing, Cheyenne, WY. vi + 340 pp., paperbound. [Keys to 120 families, 650 genera, 2369 species, 39 subspecies, and 690 varieties; 93 new combinations, 1 new species, 4 new varieties, and 1 new name; section of taxonomic notes. Available postpaid for \$13.00 from Mountain West Publishing, Cheyenne, WY 82003.]

ANNOUNCEMENTS

NEW PUBLICATIONS

HUNTER, S. C. and T. E. PAYSEN, Vegetation classification system for California: User's guide, *U.S.D.A. For. Serv., Gen. Tech. Rep.* PSW-94: i-ii, 1-12, 1986. [A system of classifying plant communities in California, with guidelines for recognizing such in the field.]

KOUTNIK, D. L., A taxonomic revision of the Hawaiian species of the genus *Chamaesyce* (Euphorbiaceae), *Allertonia*, vol. 4, no. 6, pp. 331-388, Sep 1987, ISSN 0735-8032, \$9.50 (from Publications Secretary, Pacific Tropical Botanical Garden, P.O. Box 340, Lawai, Kauai, HI 96765). [Treatment of 14 spp., 17 vars.]

A NEW SPECIES OF *SAXIFRAGA* (SAXIFRAGACEAE)
FROM THE OLYMPIC MOUNTAINS, WASHINGTON, AND
VANCOUVER ISLAND, BRITISH COLUMBIA

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ABSTRACT

Saxifraga tischii, a new species from the Olympic Mountains of Washington, and Vancouver Island, British Columbia, is described and illustrated. Distinctive features include its dwarf size, persistent chlorophyllous petals, and leaves with relatively aporous spongy mesophyll.

Recent surveys of Olympic Peninsula flora (Buckingham and Tisch 1979, 1983) have revealed the existence of a new species, herein described.

Saxifraga tischii Skelly, sp. nov.

Herba rosulata, perennis. Rhizoma breve. Laminae 5.5–17(–22) mm longae, 3.5–10(–17) mm latae, ovatae, ellipticae vel orbiculatae, supra glabratae, infra fusco-tomentosae, apicibus acutis vel obtusis, basibus cuneatis vel acutis, marginibus crenato-serratis; petioli (3–)4–10(–20) mm longi, marginibus pilosis. Caulis florifer (2–)3.5–7.5 cm altus, purpureus, glandulosus pubescentibus. Flores (3–)5–10(–18); calyx 2–4 mm longus, rotatus vel campanulatus, purpureus, dentibus ovatis vel lanceolatis (0.7–)1–2(–2.5) mm longis; petales 5–6, lanceolati vel spatulati, 1.2–2.2(–2.6) mm longi, 0.3–0.8(–1.2) mm lati, virentes vel purpurei, parce ciliati; filamenta 0.6–1.9(–2.3) mm longa; antherae roseae; styli divaricati; pedicelli 2–6 mm longi cum 0–2 bracteolis lanceolatis. Fructus purpureus, glaber, 2.3–3.5 mm longus (Fig. 1).

Rosulate perennial herb arising from short rhizome. Leaf blades 5.5–17(–22) mm long, 3.5–10(–17) mm wide, ovate, elliptical, round or rhomboidal, glabrous (rarely puberulent) above, brownish-tomentose and anthocyanic beneath, with acute to obtuse apex, cuneate to acute (rarely obtuse) base, and crenate-serrate margins, teeth 7–17; petioles (3–)4–10(–20) mm long, 1.5–3(–5) mm wide, with pilose margins. Flowering stem (2–)3.5–7.5 cm tall (in fruiting condition to 12.5 cm), purplish, glandular-pubescent, scapiform, bracteate; primary bracts lanceolate, 3–5.5(–7) mm long. Flowers (3–)5–10(–18) in small cymes; calyx 2–4 mm long, rotate to campanulate, purplish, puberulent, lobes 3-nerved, ovate to lanceolate, (0.7–)1–

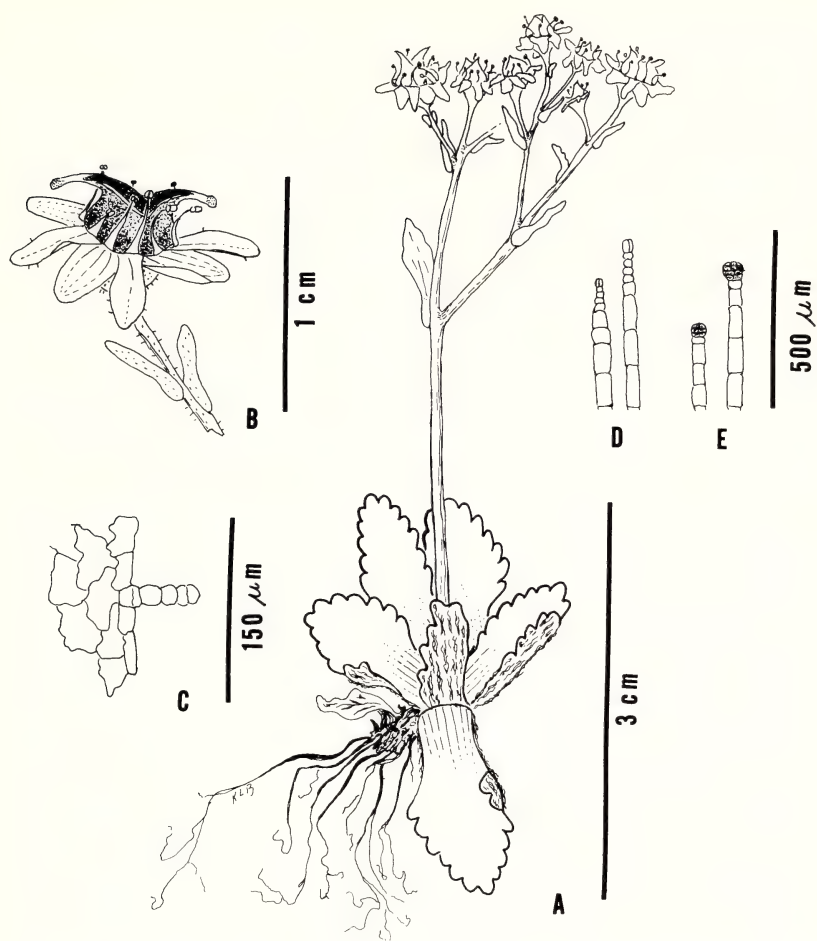


FIG. 1. *Saxifraga tischii*. A. Habit. B. Flower and pedicel. C. Cellular details of petal margin and trichome. D. Trichomes from pedicels. E. Comparable trichomes from *S. aequidentata*.

2(–2.5) mm long, with acute to rounded apices; petals 5–6, lanceolate to spatulate or oblanceolate, clawless, persistent, 1.2–2(–2.6) mm long, 0.3–0.8(–1.2) mm wide, greenish to purple, often with 1–7 cilia-like trichomes; stamens 10–12, filaments 0.6–1.9(–2.3) mm long, usually white (rarely purplish), widest at base; anthers pinkish to orange, ca. 0.3–0.5 mm wide; styles divaricate, ca. 1 mm long; pedicels 2–6 mm long with 0–2 bracteoles 1.5–3.5 mm long. Fruit purplish, glabrous, 2.3–3.5 mm long. Seeds tawny-colored, fusiform, ca. 0.6 mm long.

TYPE: USA, WA, Clallam Co.: Mt. Baldy, Olympic Mountains, T28N R4W S22, 6300 ft (1920 m), 24 Jul 1976, *Tisch 2307* (Holotype: UC).

PARATYPES: WA, Jefferson Co.: Buckhorn Mt., Olympic Mts., T27N R4W S13, 6800 ft (2070 m), 3 Aug 1984, *Tisch 2817* (WTU) and *Tisch 2818* (WS); Goat Lake area, Olympic Mts., T27N R4W S9, 6300 ft (1920 m), 18 Aug 1984, *Tisch 2897* (OSC); "Petunia Peak", Olympic Mts., T27N R4W S9, 6500 ft (1980 m), 18 Aug 1984, *Tisch 2905* (ORE); Mt. Olympus, Olympic Mts., T27N R8W S33, "8150 ft." (probably ca. 7900 ft), 13 Aug 1907, *Flett 3015* (WTU); Clallam Co.: Mt. Angeles, Olympic Mts., T29N R6W, 5 Sept 1909, *Webster 1879* (WTU); Mt. Angeles, 5500 ft (1676 m), 2 Aug 1930, *Thompson 5556* (WTU); Hurricane Ridge, Olympic Mts., 4500 ft (1372 m), 9 Jun 1934, *Thompson 10589A* (WTU). Canada, British Columbia, Vancouver Island, Castlecrag Mt., Strathcona Park, 1500 m, 9 Aug 1979, *Ogilvie and Beguin 798911* (V).

Distribution, habitat and phenology. *Saxifraga tischii* grows on ledges and in rock crevices at subalpine and alpine levels, ca. 1372–2400 m, in the Olympic Mountains, Clallam and Jefferson cos., Washington, and the interior of Vancouver Island, British Columbia. Substrates include basalt, breccia, limestone and sandstone. The plants occupy shallow (ca. 1–3 cm), well-drained soil pockets on north to northeasterly aspects, often in cirques near persistent snow patches. They flower from June to August. The chlorophyllous petals may reflect extended adaptation to the short growing seasons of these shady, microthermal environments.

Associated species include: *Anemone drummondii* Wats. var. *drummondii*, *Carex nardina* Fries, *Cystopteris fragilis* (L.) Bernh., *Douglasia laevigata* A. Gray var. *ciliolata* Const., *Draba lonchocarpa* Rydb. var. *lonchocarpa*, *Luetkea pectinata* (Pursh) Kuntze, *Luzula spicata* (L.) DC., *Poa paucispicula* Scribn. & Merr., *Ranunculus eschscholtzii* Schlecht. var. *eschscholtzii*, *Romanzoffia sitchensis* Bong., *Saxifraga caespitosa* L. var. *emarginata* (Small) Rosend., *Senecio flettii* Wieg., *Veronica cusickii* A. Gray, and *Viola flettii* Piper.

Relationships. *Saxifraga tischii* does not key well to known taxa in floras covering the Olympic Peninsula (Jones 1936, Hitchcock and Cronquist 1974), nor is it found in treatments for adjacent regions to the north (Hulten 1968, Scoggan 1978–79) and east (Davis 1952). Hitchcock (*in* Hitchcock and Cronquist 1961) discusses apetalous and purple-petaled *Saxifraga* from Mt. Olympus and vicinity, referring them to *S. occidentalis* Wats. var. *rufidula* (Small) Hitchc. Perkins (1978), who monographed the *S. occidentalis* species complex, accepted Hitchcock's interpretation and merely reassigned

the specimens to *S. aequidentata* (Small) Rosend., a synonym of the former taxon. I examined these early collections, listed here as paratypes, and found them to match the *S. tischii* holotype in all pertinent features.

The type specimens of *S. tischii*, without exception, possess tiny chlorophyllous petals with anthocyanic colorings on their margins and apices. The petals do not wither following anthesis, but remain alive and, apparently, photosynthetic through advanced fruiting. They form no visible abscission layer. Petals of *S. tischii*, in contrast with those of *S. aequidentata*, have a mesophyll-like core, stomata, and often bear multicellular trichomes (ca. 1–7) along their margins (Fig. 1). Although plants of *S. tischii* are generally smaller than those of *S. aequidentata*, developmental differences and environmental extremes produce some quantitative overlap. There are significant differences ($p < 0.001$) in petal width, filament length, number of leaf dentations, and petiole length/width ratio (Table 1). The measurements of *S. aequidentata* are largely from specimens at WTU that were annotated by Perkins and represent the range of that species.

Similarities in pistil structure, scape branching, and the general shape and dentation of basal leaves suggest that *S. tischii* and *S. aequidentata* share common ancestry within the *S. occidentalis* species complex. *Saxifraga tischii* may have evolved during the Pleistocene in mountain refugia of coastal British Columbia and/or in the Olympic Peninsula. The current restriction of *S. tischii* to cool, shady rock crevices at high elevations suggests it has limited ecological amplitude and is a highly specialized, narrowly restricted species. In the Olympics and elsewhere, *S. aequidentata* has wider distribution and occupies a variety of moderately sunny to shady environments from near sea level (e.g., near Portland, Oregon) to above 2000 m. Perkins (1978) stated that it prefers thin-soiled rock outcrops “in vernal moist, often dripping seeps”. Such environments in the Olympics (e.g., cliffs at Lake Crescent cited by Perkins 1978) usually dry out by late June, leaving the plants in a shriveled condition. *Saxifraga tischii* is semi-evergreen and carries some leaves through two growing seasons. In its normal habitats it does not shrivel after anthesis. Moreover, it grows poorly when transplanted to lower elevations. Ten cold-frame plants of *S. tischii*, kept at 650 m near Port Angeles, Washington, produced only one 2-cm (5-flowered) scape in two growing seasons. Three *S. aequidentata*, similarly located, produced eight scapes with up to 40 flowers. Under cultivation *S. tischii* retained its dwarf stature and produced typical flowers with green petals, short filaments, etc., indicating that these traits are genetically fixed. Scapes of *S. aequidentata* grew to over 12 cm and produced their normal white flowers.

Floral structure is usually more conservative and less subject to

TABLE 1. SOME MORPHOLOGICAL AND ANATOMICAL DISTINCTIONS BETWEEN *S. tischii* SKELLY AND *S. acquidentata* (SMALL) ROSEND. *From Perkins (1978).

Character	<i>S. tischii</i>	<i>S. acquidentata</i>
Petals		
Color	Green to purplish	White
Chlorenchyma	Present	Absent
Longevity	Persistent and alive through fruiting	Short-lived and mostly deciduous in fruit*
Stomata	Present	Absent
Marginal trichomes	Often 1-7/petal	Absent
Shape	Lanceolate, spatulate, oblong, oblanceolate	Ovate, oval, elliptic
Apex	Acute to rounded	Often emarginate
Base	Clawless	Often clawed
Surface (at 100×)	Non-papillose	Strongly papillose
Venation	1-nerved	Midrib usually with 2-4 lateral veins
Width	0.3-0.8(-1.2) mm, \bar{X} = 0.6 mm (n = 100)	1.3-2.2(-2.8) mm, \bar{X} = 1.7 mm (n = 100)
Stamens		
Filament length	0.6-1.9(-2.3) mm, \bar{X} = 1.3 mm (n = 180)	1.5-3.5 mm, \bar{X} = 2.7 mm (n = 180)
Filament shape	Subulate, basally flared	Often slightly clavate
Basal leaves		
Teeth on developed leaves	7-17, \bar{X} = 10 (n = 80)	13-29, \bar{X} = 19 (n = 80)
Petiole length/width ratio	1.1-5.6, \bar{X} = 3.0 (n = 70)	2.4-16.7, \bar{X} = 8.7 (n = 70)
Spongy mesophyll	ca. 120-200 μ m thick, relatively aporous	ca. 150-400 μ m thick, aerenchymatous
Flowering stems		
No. flowers/scape	(3-)5-10(-18)	To 74*
Trichomes of pedicels	Stalk cells often >6, gland 1- to 2-tiered	Stalk cells usually <6, gland often 3-tiered

evolutionary change than vegetative structure (Benson 1957, Jones and Luchsinger 1986). The minimum of 12 floral differences that separate these two species (Table 1) indicate much greater evolutionary distance than their superficial vegetative similarities may have suggested to earlier investigators.

This species is named after E. L. Tisch, my biology instructor and advisor at Peninsula College, Port Angeles, Washington.

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EVIDENCE FOR A WARM DRY EARLY HOLOCENE
IN THE WESTERN SIERRA NEVADA OF CALIFORNIA:
POLLEN AND PLANT MACROFOSSIL ANALYSIS OF
DINKEY AND EXCHEQUER MEADOWS

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ABSTRACT

Pollen and plant macrofossil analysis and ten radiocarbon dates for the sediments of Dinkey and Exchequer Meadows provide a detailed record of environmental change in the western Sierra Nevada. The Dinkey Meadow sedimentary record is nearly 5000 yr long, and the Exchequer Meadow record reaches 13,500 yr B.P. The Exchequer Meadow pollen diagram is divided into an upper *Abies* zone (0–1870 yr B.P.), a *Pinus* zone (1870–7070 yr B.P.), and a basal *Artemisia* zone (7070–13,500 yr B.P.), which is subdivided into upper *Quercus* and lower Gramineae subzones at ca. 10,680 yr B.P. The *Artemisia* zone records more xeric vegetation than occurs west of the Sierra today, and it contains *Sequoiadendron* pollen, indicating temperatures little colder than today. The presence of spores of the dung fungus *Sporormiella* indicates that grazing animals were abundant during the Gramineae subzone. A period of maximum *Abies* percentages at Dinkey, Exchequer, and other Sierra Nevada sites may result from warm dry climate shortly after 1900 yr B.P.

California's remarkable diversity of vegetation types results in large part from its topographic and climatic heterogeneity. The forests of the Coast Ranges and Sierra Nevada are separated by the grasslands of the Central Valley, and deserts occupy the rainshadow of eastern California (Major 1977). An unexpected finding of paleoenvironmental research in California is that the coastal, interior, and rainshadow areas may have had different climatic histories. During the late-Pleistocene and early Holocene, coastal California and eastern California appear to have been moister than today, whereas the western Sierra was drier (Davis et al. 1985, Davis and Sellers 1987).

At the end of the Pleistocene, mesic pine forests of coastal California were replaced by oak woodlands. Adam and West (1983) interpret the higher *Pinus/Quercus* pollen ratios from Tule Lake (West 1982) and Clear Lake (Adam et al. 1981) as indicating greater moisture and cooler temperature before 7000 yr B.P. Plant macrofossil deposits also indicate increased moisture during the early Ho-

locene (Johnson 1977), and Bergquist (1977) reports *Picea* pollen, evidence for a cool-moist climate, in sediments older than 8400 ± 100 yr B.P. at Bolinas Lagoon, near San Francisco.

In contrast, vegetation of the western Sierra during the early Holocene resembled that found east of the Sierra today. *Artemisia* pollen is abundant in early Holocene sediments from Balsam Meadow (Davis et al. 1985), Swamp Lake (Batchelder 1980), Tulare Lake in the San Joaquin Valley of California (Atwater et al. 1986), and in lower King's Canyon (Cole 1983). Comparable *Artemisia* percentages have not been duplicated in any modern pollen samples from west of the Sierran crest (e.g., Adam 1967, West 1982, Davis et al. 1985, Anderson 1987). Such high *Artemisia* percentages have been found only in vegetation east of the crest, in the Sierran rain shadow (Adam 1967, Mehringer 1967, Anderson 1987). For such vegetation to occur on the west slope of the Sierra, the climate must have been drier than today. A glacial-age expansion of the Great Basin vegetation west of the Sierra is also documented by the abundance of *Sarcobatus* pollen in the Tulare Lake core (Atwater et al. 1986).

Early-Holocene aridity is documented at other sites of interior California by low lake levels and the expansion of xeric vegetation. At Gabbott Meadow Lake (1900 m, Mackey and Sullivan 1986) near the Sierra crest, oak percentages rise from $10,500 \pm 140$ to 7570 ± 100 yr B.P. and decline until 2270 ± 80 yr B.P., probably indicating an expansion of xeric oak woodland into pine forest. At Cedar Lake, Siskiyou Co., California (1743 m, West 1986), increased aridity during the early Holocene is indicated by elevated "TCT" (Taxaceae, Cupressaceae, Taxodiaceae) percentages from 7910 ± 120 to $10,180 \pm 150$ yr B.P. Most of the TCT pollen is probably derived from *Chamaecyparis lawsoniana*, which must have become established on the moraines surrounding the lake during a period of xeric climate. Because the lake is near the coast, this aridity conflicts with interpretations for other coastal sites; alternatively, the climatic history of the northern California coast may differ from that of more southern sites. However, Cedar Lake is leeward of the Siskiyou Mountains, which reach elevations over 2100 m. If ocean fogs are responsible for the early Holocene moisture in coastal sites, the Siskiyou rain shadow may have produced a climate like that of interior sites.

East of the Sierra Nevada in the Mojave Desert, the climate was wetter at the end of the last glaciation. Glacial Lake Mojave overflowed from ca. 15,500 to 10,500 yr B.P. (Wells et al. 1987), and Searles Lake overflowed ca. 11,000 yr B.P. (Smith and Street-Perrott 1983). Packrat middens from west of Las Vegas, Nevada, contain elevated percentages of mesic shrubs and succulents, indicators of increased summer precipitation from 12,000 to 8000 years ago (Spaulding and Graumlich 1986).

Because the Sierra Nevada was a major mountain range by 3 million yr B.P. (Chase and Wallace 1986), the trans-Sierra climatic contrast has existed throughout the Pleistocene. During the last glaciation the direction of prevailing winds was probably the same as today's. Coastal sand dunes of late glacial age record wind directions equivalent to modern (Johnson 1977). Pleistocene snowlines were 600 m higher in the rainshadow of the Sierra Nevada than in adjacent mountains. This greater elevation indicates moisture patterns similar to today's patterns (Porter et al. 1983).

Purpose of the study. Pollen analysis of Dinkey and Exchequer meadows, Fresno County, California, was undertaken to confirm the early Holocene aridity of the western Sierra Nevada. This verification is particularly important because areas to the west (coastal sites) and east (desert sites) of the western Sierra record greater moisture during the early Holocene. These regional differences in climatic change are in marked contrast to traditional climatic scenarios (Antevs 1948) that call for uniform climatic change throughout western North America: cool and moist before 7000 yr B.P., hot and dry from 7000 to 4500 yr B.P. (the Altithermal), and near modern climate from 4500 yr B.P. to present.

STUDY AREA

Regional climate. Precipitation in the western Sierra is dominated by the Aleutian low, which sends cyclonic storms eastward from the Pacific Ocean during winter months (Pyke 1972). Precipitation is greatest in January and February, with a distinct period of drought in June, July, and August when dry descending air from the Pacific high covers the Pacific coast and the juxtaposition of cold, dense oceanic air and warm continental air produce the stable Pacific air mass boundary (Mitchell 1976). As cyclonic storms move westward in winter, they cross the Sierra crest, losing most of their moisture before they enter the western Great Basin.

Present vegetation. The vegetation near Dinkey Meadow (37°N, 119°10'W, 1683 m) and Exchequer Meadow (37°N, 119°5'W, 2219 m) is characteristic of the upper (Exchequer) and lower (Dinkey) Sierran Montane Forest. *Pinus murrayana* is scattered over Dinkey Meadow, which is surrounded by a mixed stand of *Abies concolor*, *Pinus jeffreyi*, *Pinus lambertiana*, and *Calocedrus decurrens*. The coring site is covered with forbs, grasses, and scattered shrubs including *Vaccinium occidentale*, *Polygonum amphibium*, *Scirpus* sp., and *Poa* spp. in wet places; and *Ribes roezlii*, *Ribes nevadense*, *Symphoricarpos parishii*, *Ceanothus leucodermis*, *Viola macloskeyi*, and *Apocynum pumilum* on the uplands.

The coring site at Exchequer meadow is wetter and is dominated

by *Carex* spp. and *Scirpus* spp. Scattered *Pinus murrayana* grow on the meadow, which is surrounded by *Pinus jeffreyi* and occasional *Abies magnifica*. *Ribes roezlii* and *Ribes nevadense* are common understory plants in the forest.

Glacial deposits. The western Sierra was glaciated extensively during the late Pleistocene, and Matthes (1960) mapped glacial deposits nearly down to the elevation of Dinkey Meadow ca. 1700 m. Although we know of no detailed maps of glacial deposits for the area, Matthes' (1960) maps indicate that Dinkey Meadow was beyond the terminal moraine, and Exchequer Meadow was adjacent to, but not covered by, the Dinkey Creek glacial lobe (Fig. 1).

METHODS

The sediments of Dinkey and Exchequer Meadows were cored on September 1, 1985. The wettest portions of the meadows were chosen for coring to avoid oxidation or loss of sediment due to drying.

Sampling techniques. At Exchequer Meadow the upper 124 cm of sediment was collected with a 5 cm diameter square rod piston sampler (Wright 1967), and the lower sediment was cored with a 2.5 cm diameter Dachnowsky corer (Faegri and Iversen 1975) to 399 cm depth. The entire 300 cm Dinkey Meadow core was recovered with the piston sampler except for the interval from 210 to 230 cm, which was recovered with the Dachnowsky.

The cores were wrapped in plastic film and aluminum foil, and were stored at 1°C prior to sampling. Volcanic ash layers were submitted to Andrei Sarna-Wojcicki, U.S. Geological Survey, Menlo Park, California, for identification. Radiocarbon samples were submitted to Beta Analytic, Coral Gables, Florida.

Radiocarbon dates. All ten radiocarbon samples (Figs. 2 and 3) were adjusted for $^{13}\text{C}/^{12}\text{C}$ fractionation, and samples Beta-16113 and Beta-17185 from Exchequer Meadow were given extended counting times because they contained small amounts (0.20 and 0.35 g, respectively) of carbon. For Dinkey Meadow the sedimentation rate changed from 0.08 cm yr⁻¹ to a slower 0.05 cm yr⁻¹ below 150 cm (Fig. 2). For Exchequer Meadow the sedimentation rate was nearly constant (0.03 cm yr⁻¹) from the surface to the base of the core (Fig. 3).

Pollen extraction. Pollen extraction followed standard procedures (Faegri and Iversen 1975). The samples (volume 1 cm³) were placed in 10% HCl and *Lycopodium* tracers were added to permit calculation of pollen concentration. After screening, the samples were treated with concentrated HCl and left overnight in 40% HF to remove carbonates and silicates. The samples were acetolyzed to

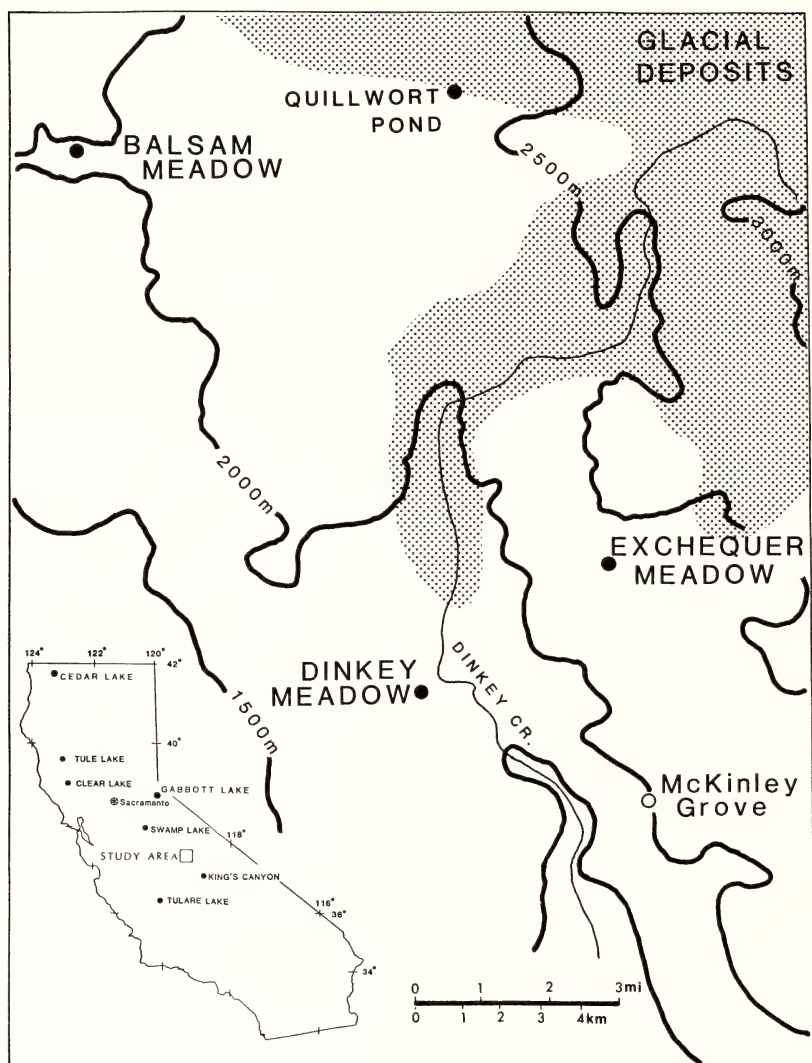


FIG. 1. Map of Dinkey and Exchequer Meadows area showing extent of late-Pleistocene Glaciation (stippled pattern). Inset shows location of California sites mentioned in text.

remove cellulose and similar organic compounds, and treated with 10% KOH to remove humates. After staining, the samples were transferred to glycerin.

Pollen identifications were based on the reference collection and

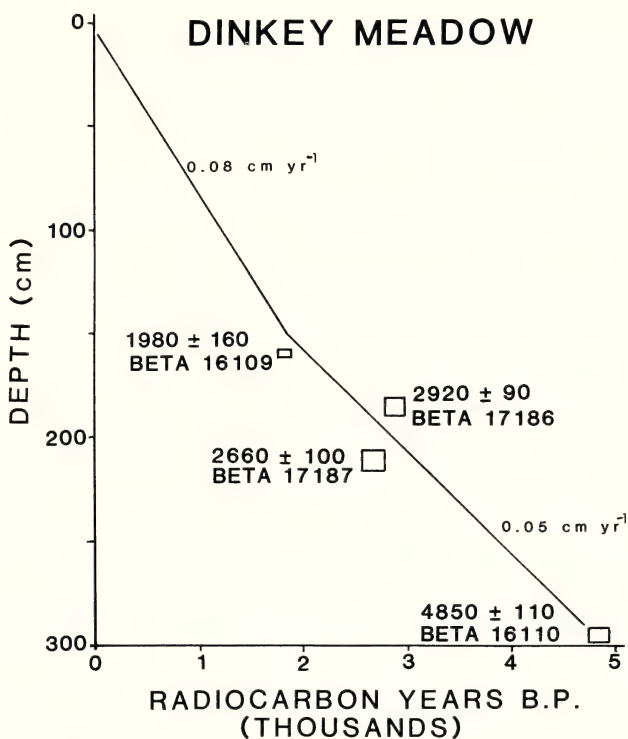


FIG. 2. Graph of Dinkey Meadow radiocarbon dates versus sediment depth. Solid line shows least squares regression of dates on sediment depth below 150 cm; above this depth it is connected directly to the surface. Height of squares is sample interval, width is date \pm one standard deviation.

library at the University of Arizona Palynology Laboratory. The pollen sum (divisor for percentage calculations) does not include aquatics; e.g., *Salix* or Cyperaceae, or spores. The following notes apply to the types shown on the pollen diagrams (Figs. 4 and 5): Cupressaceae may include some Taxaceae and Taxodiaceae except *Sequoiadendron*. Ericaceae includes mostly *Arctostaphylos* but at least one other type was seen. "Other Compositae" includes all pollen of that family excluding *Ambrosia*, *Artemisia*, *Cirsium*, and Liguliflorae.

Plant macrofossils. The sediment from both sites was suspended in water and screened to remove fine inorganic particles. Identifiable remains (seeds, needles, and large pieces of wood) were removed from the matrix under 7–45 \times magnification. Conifer needles were sectioned to permit species identification, and the abundance of

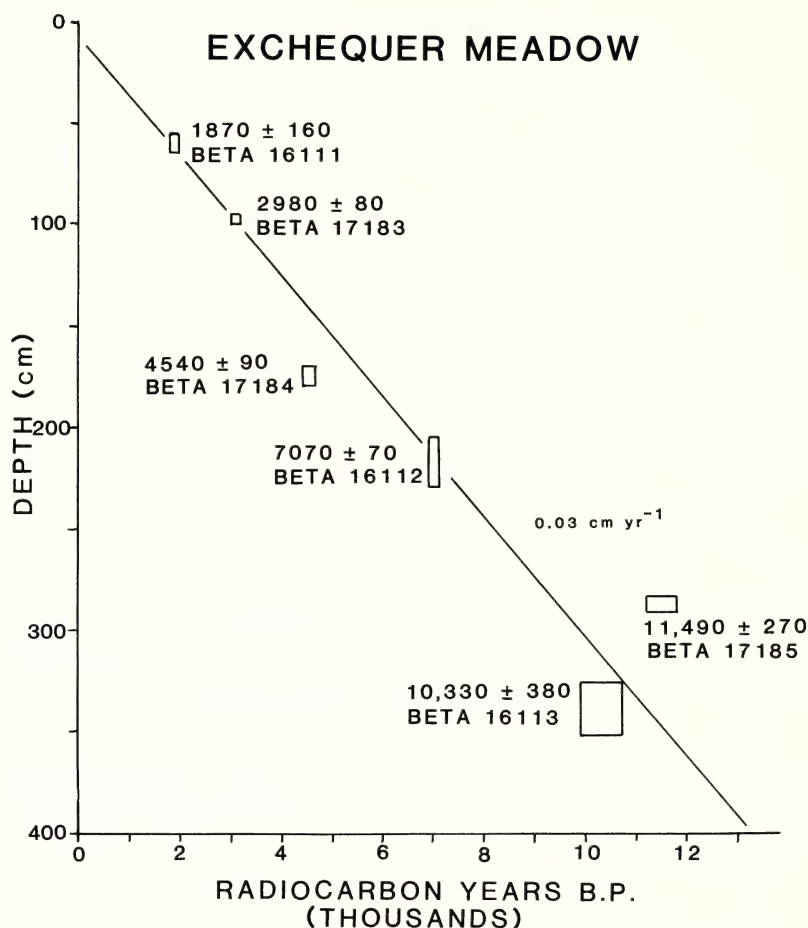


FIG. 3. Graph of Exchequer Meadow radiocarbon dates versus sediment depth. Solid line shows least squares regression of dates on sediment depth. Height of squares is sample interval, width is date \pm one standard deviation.

charcoal was noted on a scale of zero (absence) to four (very abundant).

RESULTS

The Dinkey Meadow sediments are yellowish brown (10YR 5/4, Munsell color) to very dark gray (5YR 3/1) peat down to 69 cm; and dark gray (10YR 4/1) medium sand to the base of the core. A volcanic ash layer is present at 39–40 cm. Exchequer Meadow sediments are less homogeneous. They are primarily peat down to 101

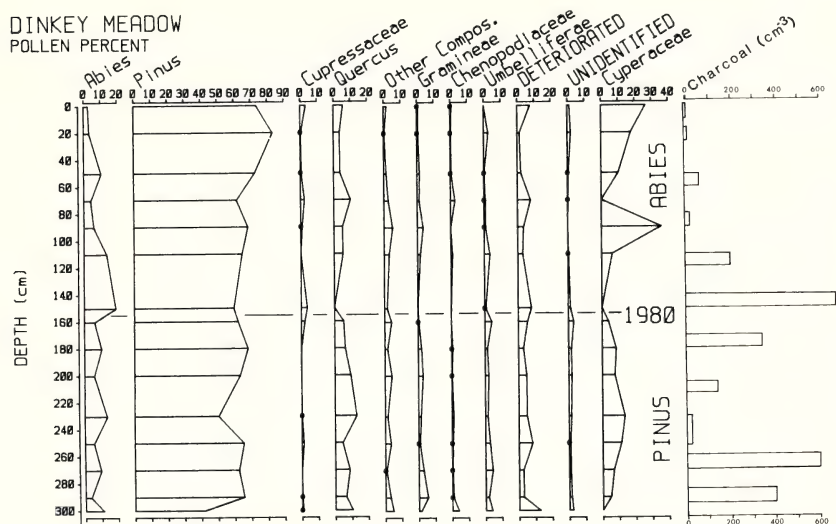


FIG. 4. Dinkey Meadow pollen diagram for abundant pollen types plotted versus sample depth. Dots are for percentages less than 2%. Cyperaceae and other aquatics are outside the pollen sum, *Pinus* is in the sum. Pollen zones and ages of boundaries shown on right. Vertical width of charcoal histograms shows width of sediment sample interval.

cm, interbedded sand and peat to 290 cm, and alternating fine and coarse sand down to 399 cm. Two volcanic ashes are present at Exchequer Meadow: one at 50–54 cm; the other at 169–170 cm; The 54 cm Exchequer Meadow ash, the only one suitable for identification, was identified as a “young Inyo Crater Ash.”

Dinkey Meadow. The Dinkey Meadow pollen diagram (Fig. 4) shows relatively little change, which is not surprising given its relatively brief (<5000 yr) record. *Pinus* is the most abundant pollen type (50–83%), followed by *Abies* (4–19%) and *Quercus* (0–13%). The percentages of *Abies* are lower and the percentages of *Quercus* are higher than at Balsam Meadow, which is consistent with the lower elevation (2040 vs. 1683 m) of Dinkey Meadow. The age of maximum *Abies* pollen percentages (Fig. 4) at Dinkey Meadow (1980 ± 160) is very close to estimated age of maximum *Abies* percentages (1710 yr B.P.) at Balsam Meadow.

The plant macrofossils from Dinkey Meadow (Table 1) provide additional data for paleoenvironmental reconstructions. All of the conifer species now at the site are present as plant macrofossils. *Pinus murrayana* needles are the most abundant macrofossil, but other conifers are absent above 100 cm. The sediments from 100–170 cm, which contain maximum *Abies* pollen percentages, contain

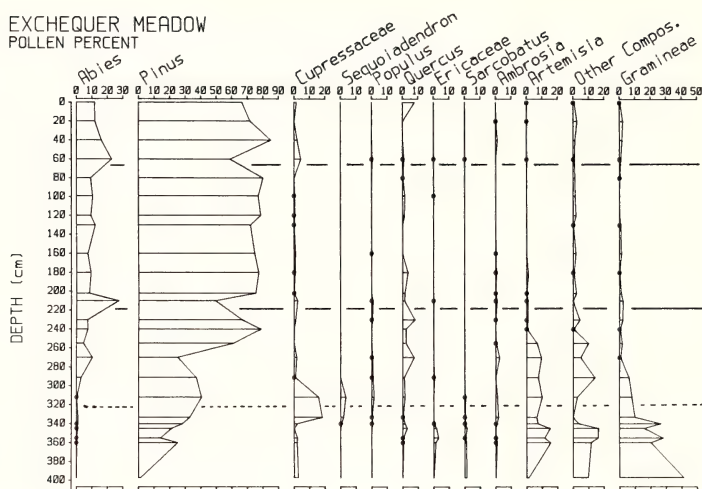


FIG. 5. Exchequer Meadow pollen diagram for abundant pollen types plotted versus sample depth. Dots are for percentages less than 2%. Cyperaceae and other aquatics are outside the pollen sum, *Pinus* is in the sum. Pollen zones and ages of boundaries shown on right. Vertical width of charcoal histograms shows width of sediment sample interval.

both *Abies concolor* and *Abies magnifica* needles, so both species could have contributed to the *Abies* pollen maximum. The *Abies magnifica* needles in the 110–120 cm sample, however, are the only remains of this species in the core. Charcoal abundance (Fig. 4) shows two peaks: one at 170–180 cm (2365 yr B.P.) just before maximum *Abies* pollen percentages, and the other at 260–270 cm (ca. 4180 yr B.P.). This trend in charcoal concentration is similar to that at Balsam Meadow (Davis et al. 1985).

Exchequer Meadow. The pollen zones for Exchequer Meadow (Fig. 5) are the same as those for Balsam Meadow (Davis et al. 1985) demonstrating the regional nature of the vegetation change, but the beginning of the *Abies* zone is later (1870 ± 60 yr B.P.) than at Balsam Meadow (3000 yr B.P.). The age of maximum fir percentages, however, is nearly the same at Exchequer (1870 ± 70), Dinkey Meadow (1980 ± 160) and Balsam Meadow (1710 yr B.P.). The boundary between the *Pinus* and *Artemisia* zones at 7070 ± 70 yr B.P. is synchronous with this transition at Balsam Meadow, but the basal *Artemisia* zone is longer, and is subdivided into upper *Quercus* and lower Gramineae subzones at ca. 10,680 yr B.P. In the Gramineae subzone percentages of *Sequoiadendron*, Gramineae, *Cas-tilleja*, and Cruciferae are greater than any at Balsam Meadow.

The diversity and concentration of plant macrofossils at Exchequer Meadow is less than at Dinkey Meadow. Sedge (*Carex*) remains

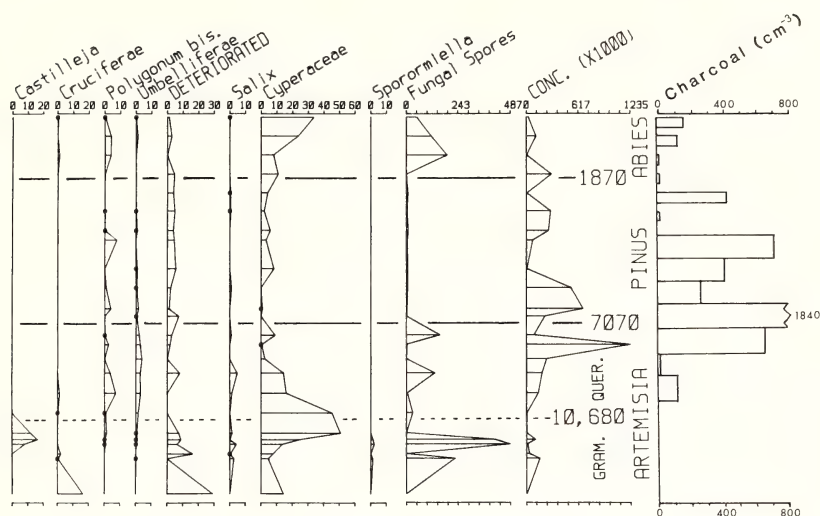


FIG. 5. Continued.

are the most abundant type. The *Abies* needles were preserved too poorly to identify to species, but *Abies* sp. and *Pinus murrayana* remains were present in surface sediment (Table 2). Charcoal fragments reach peak abundances at 80–90 cm (2740 yr B.P.), 124–129 cm (4140 yr B.P.), and 199–244 cm (7350 yr B.P.), a sequence similar to that at Balsam Meadow.

DISCUSSION

Paleoclimatology. An *Abies* pollen maximum shortly after 1900 yr B.P. is present at all three sites we have studied in the area. This event follows the general initiation of meadow development in the western Sierra (Wood 1975) that accompanied the beginning of Neoglacial cooling ca. 3000 years ago. Nineteen hundred yr B.P. is recognized as an interval of glacier retreat within the Neoglacial in western North America (Porter and Denton 1967), but Scuderi (1984) states that glaciers in the high Sierra Nevada may have advanced at this time (1850 yr B.P.). Nineteen hundred yr B.P. falls between periods of cool moist climate recorded in the growth of bristlecone pine in the White Mountains of eastern California (LaMarche 1978).

At Balsam and Dinkey Meadows macrofossils of *Abies concolor* and *A. magnifica* are present during the *Abies* pollen maximum (Table 2, Fig. 5). Today, these species do not grow on the bogs. Both white and red fir are characteristic of relatively dry slopes (Munz 1959), so the invasion of the meadows 1900 yr B.P. may indicate a period of warm, dry climate when the bogs dried. The Exchequer Meadow core was taken near the edge of the meadow; consequently,

TABLE 1. DINKEY MEADOW PLANT MACROFOSSIL CONCENTRATIONS (100 cm⁻³).

Sample interval	0-10	17-27	50-60	80-90	110-120	140-150	170-180	205-215	232-256	260-270	285-295
<i>Abies magnifica</i> needles	0	0	0	0	3	0	0	0	0	0	0
<i>Abies concolor</i> needles	0	0	0	0	0	0	3	0	0	3	0
<i>Abies</i> undif. needles	0	0	0	0	1	0	0	0	0	4	1
cf. <i>Calocedrus</i> bract	0	0	0	0	2	0	0	0	0	0	0
<i>Pinus jeffreyi</i> seed	0	0	0	0	0	0	0	0	0	0	1
<i>P. lambertiana</i> needle	0	0	0	0	1	0	0	0	0	0	0
<i>P. murrayana</i> needles	12	4	0	0	6	4	0	0	1	140	323
<i>P. murrayana</i> cones	0	0	0	0	0	0	1	0	0	1	3
<i>P. murrayana</i> seed	0	0	0	0	1	0	0	0	0	0	0
<i>Sambucus</i> seed	0	0	0	0	0	0	0	0	0	1	0
<i>Viola</i> seeds	0	1	0	0	0	0	2	0	0	29	0
<i>Carex</i> lenticular	20	0	1	0	1	0	2	1	0	6	0
<i>Carex</i> trigonous	1	0	0	1	1	0	0	0	0	6	3
<i>Potamogeton</i> seeds	0	0	2	0	5	0	0	0	0	1	0
Unidentified seeds	0	0	0	0	0	0	2	2	0	0	1
<i>Isoetes</i> megaspore	0	0	0	0	1	0	0	0	0	0	0
Unidentified wood	0	0	8	12	5	6	3	2	3	74	102
Charcoal >0.5 mm	5	16	58	19	180	683	365	132	23	589	372
Moss stems	1	0	0	0	0	0	0	0	0	0	0
Insect parts	6	0	0	1	0	0	1	0	0	0	1
Fecal pellets	0	0	0	0	6	12	0	9	0	9	2
Volume sediment cc	100	100	100	100	100	100	100	100	231	100	100

its surface sediment contains fir macrofossils. During the fir pollen maximum, sedge pollen percentages are low at Dinkey Meadow (Fig. 4), and sedge macrofossils are absent in Exchequer Meadow sediments (Table 2), perhaps indicating meadow desiccation.

A date of 1920 ± 50 yr B.P. (A-4428) at 64–70 cm marks a transition from inorganic to organic sediments at Quillwort Pond (Fig. 1). *Isoetes* megaspores are present throughout the 1 m core, but below 70 cm pebbles are abundant and plant macrofossils are absent. Above 70 cm *Potamogeton* and *Carex* are common, and conifer needles and seeds are abundant (up to 12 *Abies* needles cm^{-3}). Thus, the date marks the beginning of encroachment of trees and emergent aquatics into the Quillwort Pond basin.

Sites at higher elevation do not consistently show the *Abies* pollen maximum (Anderson 1987), so its importance may be limited to low elevation sites (below 2400 m?) where precipitation is less.

An "early Holocene Xerothermic." The classical climatic sequence for western North America calls for greatest temperatures and lowest moisture 7000–4500 yr B.P. during the "Altithermal" of Ernst Antevs (1948). This chronology was never accepted universally (Aschman 1957, Martin 1963), and many authors (Kearney and Luckman 1983, Ritchie et al. 1983, Hebda and Mathewes 1984, Davis et al. 1985, 1986, Elias 1985, Vance 1985) have found evidence for a much earlier thermal maximum centered ca. 10,000–8000 yr B.P., *before the beginning of the classical Altithermal*.

Many of the studies documenting the "early Holocene Xerothermic" (a phrase proposed by Hebda and Mathewes 1984), have been of sites at high elevation (Kearney and Luckman 1983, Elias 1985) or at high latitudes (Ritchie et al. 1983) where summer temperature controls the position of tree line. Due to the changing relationship of the perihelion and the summer solstice, insolation during summer months (June, July, August) was greatest in the northern hemisphere prior to 7000 yr (Davis et al. 1986). Although the actual change in insolation is small, atmospheric circulation is very sensitive to even small changes in insolation. General Circulation Models (e.g., Sellers 1984, Kutzbach and Guetter 1986) indicate summer temperature 9000 yr B.P. were 1–2° C warmer than today.

Previous paleoenvironmental studies in the western Sierra Nevada have demonstrated maximum aridity in the early Holocene ca. 7000–10,000 yr B.P. (Davis et al. 1985). The data from Exchequer Meadow corroborate this finding, providing support for the contrast between western Sierra climate and that of regions to the west and east. The early-Holocene sediments from Exchequer Meadow also contain the pollen of species that are today near their upper-elevational limits, indicating that temperatures were not much colder than today, thereby supporting the findings of Kearney and Luckman (1983), Ritchie et al. (1983), and Elias (1985) based on the position of upper treeline.

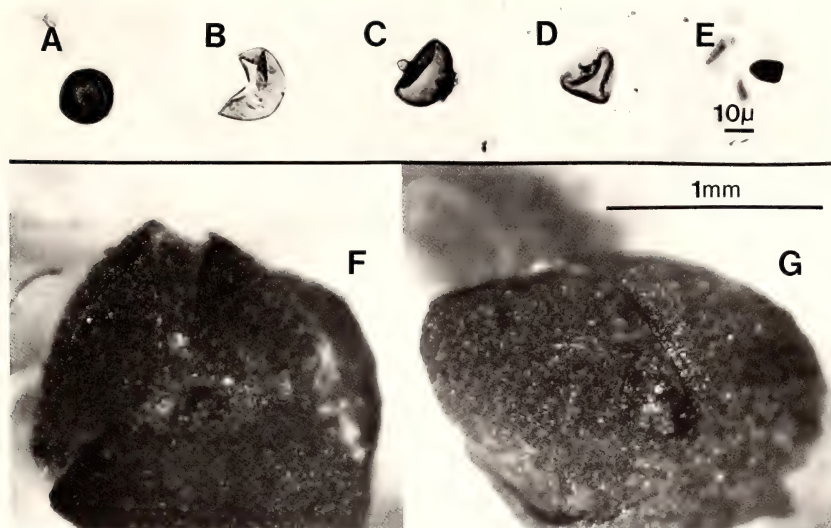


FIG. 6. A-D. Pollen from Exchequer Meadow, 312 cm *Artemisia* (A), Cupressaceae (B), *Sequoiadendron* (C-D); E. *Sporormiella* spore (Exchequer Meadow, 345 cm); F-G. terminal bud of *Calocedrus* or *Juniperus* (Exchequer Meadow, 274-299 cm).

At Exchequer Meadow, *Sequoiadendron* pollen is present from 312-340 cm and a cf. *Calocedrus* or *Juniperus* macrofossil is present at 274-299 cm (Fig. 6). Both *Sequoiadendron* and *Calocedrus* (now at 1400-2560 m and 730-2500 m respectively, Munz 1959, 1968) would be near their upper elevational limit at Exchequer Meadow (2219 m), and neither are present there today. The nearest *Sequoiadendron* grove to Exchequer Meadow today is the McKinley grove, 5 km south at 1951 m elevation (Fig. 1).

A series of environmental factors influence the distributions of plant taxa. Soil moisture and fire frequency are particularly important for the regeneration of *Sequoiadendron*. But in general, the upper elevational limits of plants are set by temperature (Daubenmire 1943). For these species to have been present near their current upper-elevation limits during the early Holocene, temperatures could not have been much colder than today.

Cole (1983) has documented the presence of *Sequoiadendron* pollen and *Calocedrus* macrofossils from 14,190 to over 45,000 yr B.P. in packrat middens from 980 to 1280 m elevation in Kings Canyon (Fig. 1). It appears that these species also were more widespread at low elevation during the late-glacial and early Holocene.

Prior to the expansion of *Sequoiadendron*, the vegetation near Exchequer meadow probably resembled Crucifereae-dominated al-

pine grassland that today occurs on dry open areas with raw soil (Major and Taylor 1977, p. 629). The dearth of tree pollen and abundance of herb pollen, particularly *Castilleja* and Cruciferae (Fig. 5) indicate alpine vegetation. We infer a rapid climatic warming ca. 11,000 yr B.P.

The absence of spores of the dung fungus *Sporormiella* in sediments younger than ca. 11,000 yr B.P. at Exchequer Meadow may date the extinction of the Rancholabrean megafauna in the western Sierra. The spores are not present in Holocene sediments, but are abundant (2.3%, 32 grains $\text{cm}^{-2} \text{yr}^{-1}$) in sediments below 340 cm (Fig. 5) equivalent to an age of 11,600 yr B.P. (Fig. 3). *Sporormiella* spores (Fig. 6) are abundant in modern sediments only where introduced grazing animals are plentiful, and they are even more profuse in sediments older than 11,000 yr B.P. in several sites (Davis 1987). The spores are linked directly to extinct animals by their presence in mammoth dung (Davis et al. 1984). Although *Sporormiella* spores are not restricted to extinct animals, their presence in late-Pleistocene sediments at Exchequer Meadow and other sites appears to record a declining abundance of grazing animals at the end of the Pleistocene.

CONCLUSIONS

The pollen and macrofossil records from Exchequer Meadow indicate vegetation during the early Holocene resembling that found east of the Sierra Nevada today. These records corroborate earlier findings of aridity in the western Sierra at a time when areas to the west and east were relatively moist, concurrent with the extinction of Pleistocene megafauna in the area. Modern climatic contrasts between coastal, interior, and rainshadow regions play an important role in the vegetational differences among these areas. Paleovegetation data from Exchequer Meadow and other sites indicate different climatic and vegetational histories for these areas during the late Quaternary. These paleoclimatic differences also may have played a role in the differentiation of these vegetation types.

ACKNOWLEDGMENTS

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ANNOUNCEMENT

NEW PUBLICATION

STIEBER, M. T., A. L. KARG, M. WALKER, G. D. R. BRIDSON, H. M. BURDET, M. M. CHAUTEMPS, and T. MORUZZI-BAYO (compilers), *Catalogue of portraits of naturalists, mostly botanists, in the collections of the Hunt Institute, The Linnean Society of London, and the Conservatoire et Jardin Botaniques de la Ville de Genève*, pt. 1, *Group portraits*, Hunt Institute for Botanical Documentation, Carnegie-Mellon Univ., Pittsburgh, PA 15213, 1987, xi, 93 pp., unillus., ISBN 0-913196-50-9 (paperbound), \$9.00 (for U.S. and Canada, from preceding address; from elsewhere order from Wheldon & Wesley, Lytton Lodge, Codicote, Hitchin, Herts. SG4 8TE, England).

ANNOUNCEMENT

TWELFTH GRADUATE STUDENT MEETINGS

The California Botanical Society will sponsor the Twelfth Graduate Student Meetings on 29 October 1988 at San Jose State University.

The presentation categories (proposed research, research in progress, and finished research) allow the sharing of ideas and knowledge within the graduate student community. Awards for each of these categories will be presented at the banquet on 29 October.

For information contact Valerie Haley, Graduate Student Representative, Department of Biological Sciences, San Jose State University, San Jose, CA 95192.

SPECIES FREQUENCY IN RELATION TO TIMBER HARVEST METHODS AND ELEVATION IN THE PINE TYPE OF NORTHEAST CALIFORNIA

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ABSTRACT

Few trends in species presence and frequency due to different timber harvest treatments were apparent 40 years after logging in the pine type of northeastern California. *Ceanothus prostratus* was generally absent from units where all trees larger than 29.5 cm dbh had been removed 40 years ago. *Calocedrus decurrens* was more frequent in uncut control plots. Species richness was constant across the area. Differences in species frequencies among experimental blocks located at five elevations suggested at least two major plant communities within the forested zone, with elevation a major environmental influence. A list of common plant species and their frequencies are provided for the Blacks Mountain Experimental Forest in northeastern California.

The pine type of northeastern California has received minimal botanical study. It has been described as the eastside phase of mixed conifer forest (Griffin and Critchfield 1972), yellow pine forest by Munz (1973), interior ponderosa pine by the Society of American Foresters (Barrett et al. 1980), and eastside pine type by McDonald (1983). Vasek (1978) studied forests dominated by *Pinus jeffreyi* between 1280 and 1950 m elevation. He noted that these forests ranged along moisture and temperature gradients across the region, with local variation influenced by elevation, aspect, surface rock and soil depth. In higher montane forests, Rundel et al. (1977) suggested that *Calocedrus decurrens* and *Abies concolor* have both increased their relative and absolute densities since the turn of the century when fire control programs went into effect. Logging and widespread grazing may have caused compositional changes.

At the Blacks Mountain Experimental Forest, the U.S. Forest Service has undertaken several long-term studies on the growth and harvest of the major tree species: *Pinus ponderosa*, *Pinus jeffreyi*, *Abies concolor*, and *Calocedrus decurrens* (Hallin 1959, Robson and Standiford 1983). Roy (1946) studied the sagebrush flats within the Experimental Forest. A list of the most abundant range plant species has been compiled for nearby Harvey Valley Range Allotment (Hormay 1959). Similar lists are available for the California State University at Chico field station at Eagle Lake (R. Schlising pers. comm.). Hormay (1940) documented some impacts of logging on forage

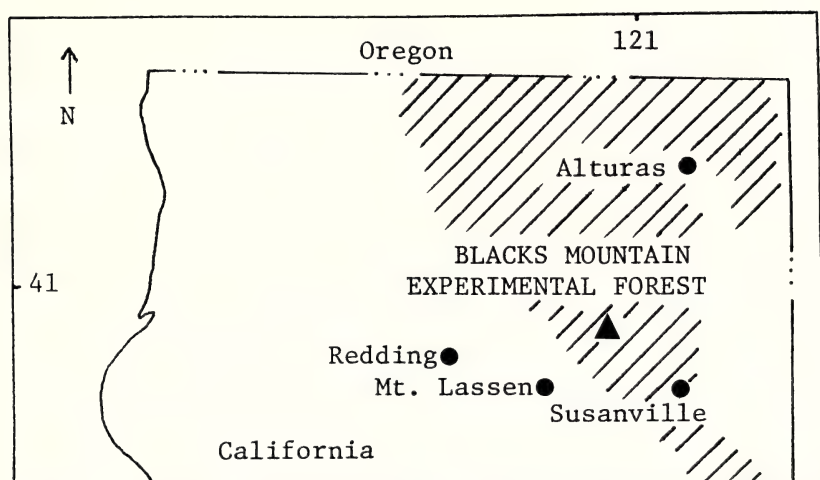


FIG. 1. Location of the Blacks Mountain Experimental Forest and pine type of northeast California (diagonal lines) (Hallin 1959).

plants. The impacts of cattle grazing on *Purshia tridentata* have been studied extensively (Hormay 1943, Neal 1982).

Hallin (1959) stated that the Blacks Mountain Experimental Forest is representative of the pine type of northeastern California. As a study site, it provided the opportunity to examine the presence of understory species in relation to well-planned and documented timber harvest research. I undertook exploratory analyses to identify differences in species frequency due to timber harvest methods 40 years after logging, and to note changes in species presence with elevation.

STUDY SITE

The Blacks Mountain Experimental Forest is located in the Lassen National Forest, Lassen Co., California (Fig. 1). Approximately half of the study site lies in a gently rolling basin; the remainder extends up moderate slopes to the north and east. Elevations range from 1700 to 2100 m. The Forest is composed of a mosaic of small, even-aged groups of trees of various ages that vary in size from a fraction of a hectare to 4 ha, and by scattered older trees in younger stands (Hallin 1959). Forest gaps, or openings, are characteristic of these forests (Franklin and Dyrness 1973).

Hallin (1959) reported that the mean annual precipitation varied from 23 to 74 cm, and averaged 46 cm during the period 1935–53. About 90% of the precipitation falls in the months of October through May. McDonald (1983) and Franklin and Dyrness (1973) state that

soil moisture becomes depleted rapidly and warm summer temperatures and low humidity increase evapotranspiration to the point of creating moisture-deficient soil. Consequently, the growing season for an average ponderosa pine (*Pinus ponderosa*), for example, lasts only from 1 May to about 15 June in a typical year. Seasonal browsing or grazing of plants by herbivores occurs between May and October.

METHODS

Hallin (1959) described timber harvest studies initiated in 1938. A randomized block design with six treatments was used. Four to six treatments were randomly allocated to 8-ha macroplots within each block (Fig. 2). Treatments (listed by increasing intensity of cut) were: (1) control (C)—no cutting; (2) sanitation salvage (IS)—removal of diseased, dead and dying trees; (3) unit area control (UAC)—group selection removal of aggregations of mature trees combined with sanitation salvage in the stand; (4) moderate selection (MFS)—approximately 55% of the volume cut; (5) heavy selection (HFS)—approximately 75% of the volume cut; and (6) "clear-cut" (CC)—removal of trees 29.5 cm dbh and greater and natural regrowth. Timber harvesting discriminated against *Abies concolor* and *Calocedrus decurrens* (a greater percentage of trees of these species were removed compared to pine species).

I sampled five blocks that represented site elevations (Fig. 2). Experimental design, however, did not control for variables such as slope, aspect, soil depth and stoniness, and seed source. No major soil differences were apparent among the blocks based on profile descriptions in a soil survey (Storie et al. 1940). Three blocks [39, 40, and 42 (the number represents the year of logging)] included all six treatments, whereas the IS and CC treatments were absent from two blocks (43 and 47).

Ten 25-m² microplots were located randomly along a transect within each macroplot. A species list was recorded for each microplot and from this frequency per 25 m² (frequency) estimated for each macroplot. Plant nomenclature was based on Munz (1973). It was not feasible to compile a complete list in the field. I was not able to identify several species found without flowers. Individual plants often lacked inflorescences when I visited the microplots. Cattle grazing contributed to this problem in several areas. Therefore, I was unable to gather data on frequency of occurrences of grasses, penstemons, and a few other species. *Pinus ponderosa* and *P. jeffreyi* were sampled and analyzed as one species because of potential hybridization and difficulty in separating the two in field identification (Vasek 1978). Sampling was done between June and August 1983. This period followed an unusually wet winter for the region (167%

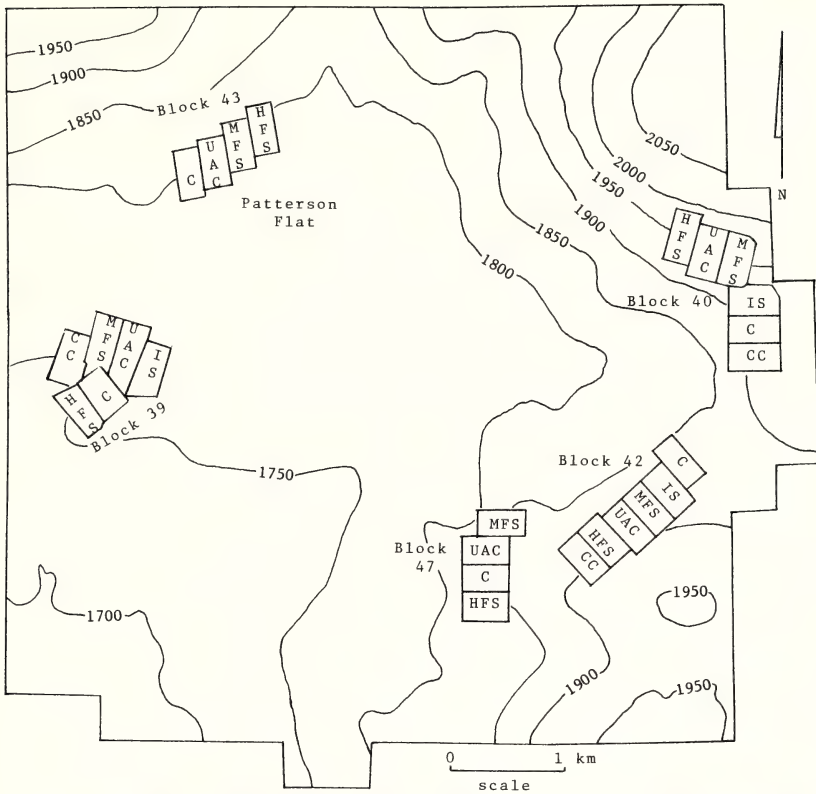


FIG. 2. Elevation contours (m), cutting blocks, and treatment units (C = control; IS = sanitation salvage; UAC = unit area control or group selection; MFS = moderate selection; HFS = heavy selection; CC = clear cut).

of normal precipitation occurred at a U.S. Forest Service weather station at 1390 m, and located 58 km to the southeast).

There was a total of 26 macroplots within the five blocks, and frequency studies were based on these twenty-six 8-ha units (Fig. 2). I performed analyses of variance (ANOVA) to identify differences ($p < 0.05$) among harvest treatments and among blocks.

RESULTS

Ninety-five species were identified within the 330 microplots. The woody plants, especially the trees, dominated cover or biomass. In terms of numbers of species, the dominant plant families were Asteraceae (17 species, 18%), Poaceae (11 species, 12%), and Scrophulariaceae (12 species, 13%). Consideration also of species frequency

would have added Pinaceae, Rhamnaceae, Laminaceae, Rubiaceae, Ericaceae, Cupressaceae, and Rosaceae to the list of major plant families. The overall (all 26 macroplots) standard deviation of mean frequency of major species ranged from 5 to 20%; variances were greater within each treatment or block.

Few trends in species presence and frequency due to timber harvest treatments were apparent 40 years after logging (Table 1). Pine species frequency was lower in the CC treatment, but not significantly different ($p = 0.11$) from the control. *Ceanothus prostratus* was generally absent from the CC treatment ($p = 0.02$). *Calocedrus decurrens* was more frequent in control plots, but frequencies were not statistically different from other treatments ($p = 0.19$).

Species richness ranged from 27 to 37 per block. Frequency of species of Poaceae lumped together was higher in the lower elevation blocks (ANOVA $p = 0.02$).

Field observation and examination of the block data in Table 2 suggest that Blacks Mountain Experimental Forest is located in a transition zone between two major plant communities. Table 2 lists the plant species that characterize the two communities, including those that were significantly different among blocks. The lower elevation community (below approximately 1800 m) is typical of what is commonly referred to as eastside pine or interior ponderosa pine, with the overstory dominated almost exclusively by *Pinus ponderosa* and *P. jeffreyi*, and the understory dominated by *Purshia tridentata* and *Artemisia tridentata*. Frequency of finding one plant of the Poaceae in a 25-m² plot was 100%. The overstory in the higher elevation community is characterized by the same two pine species and two additional conifers, *Abies concolor* and *Calocedrus decurrens*. Typical understory species are *Symphoricarpos vaccinoides* and *Monardella odoratissima*. Frequency of finding one plant of the Family Poaceae in a 25-m² plot was 70%.

DISCUSSION

Vasek (1978) observed that despite logging, the forests of the southern Modoc Forest had considerable resemblance to pristine vegetation. Few differences in species frequency were observed on Blacks Mountain 40 years after logging. Perhaps the plants of this forest are adapted to a disclimax state. Prior to 1900, insects and fire maintained forests in a variety of successional stages. Pine mortality caused by western bark beetle (*Dendroctonus brevicomis*) is still heavy (Hallin 1959, Hart 1983). Fire frequencies of 6–36 years are reported in the Lava Beds National Monument [110 km to the north by Johnson and Smathers (1976) and Martin and Johnson (1979)], and eastern Oregon by Soeriaatmadja (1966). Logging and grazing by cattle and sheep have influenced succession over the past

TABLE 1. PLANT SPECIES FREQUENCY IN 40-YEAR-OLD CUT UNITS ON BLACKS MOUNTAIN EXPERIMENTAL FOREST. Means are presented for common species (>5% overall mean frequency) for each treatment and block, and are estimated from 10 25-m² plots in each 8-ha unit. A dash (—) indicates frequency <1%. Treatment codes: C = control; IS = sanitation salvage; UAC = unit area control; MFS = moderate selection; HFS = heavy selection; CC = "clear-cut". IS and CC treatments were absent from blocks 43 and 47. Block numbers refer to the year they were cut, and are listed in ascending elevation (39—1750 m, 43—1800 m, 47—1830 m, 42—1875 m, and 40—1920 m).

No. of cutting units	Treatment						Block				
	C	IS	UAC	MFS	HFS	CC	39	43	47	42	40
	5	3	5	5	5	3	6	4	4	6	6
<i>Abies concolor</i>	44	53	46	54	52	63	—	10	72	85	82
<i>Arabis holboellii</i>	6	17	22	20	10	30	—	—	28	29	25
<i>Arctostaphylos patula</i>	26	7	10	22	34	7	10	45	65	21	33
<i>Artemisia tridentata</i>	2	—	8	6	12	33	40	—	—	—	—
<i>Calocedrus decurrens</i>	50	17	30	22	32	13	—	20	80	28	32
<i>Castilleja applegatei</i>	8	7	20	18	16	10	5	13	25	12	18
<i>Ceanothus prostratus</i>	68	57	78	68	54	3	47	85	90	52	52
<i>Ceanothus velutinus</i>	6	—	14	16	4	7	—	—	25	18	2
<i>Chrysothamnus</i>											
<i>nauseosus</i>	8	6	10	22	16	20	40	10	5	3	7
<i>Collinsia torreyi</i>	18	13	30	32	30	40	38	43	15	23	18
<i>Crepis acuminata</i>	2	7	2	8	10	—	2	23	—	5	—
<i>Cryptantha affinis</i>	8	10	20	18	10	30	2	—	3	3	15
<i>Eriophyllum lanatum</i>	16	20	22	34	28	27	8	27	33	20	38
<i>Fritillaria atropurpurea</i>	6	17	22	18	10	3	—	—	5	17	2
<i>Gayophytum humile</i>	8	—	8	14	10	33	20	28	—	5	7
<i>Hieraceum albiflorum</i>	10	7	24	18	17	7	—	—	25	21	15
<i>Lupinus caudatus</i>	24	20	18	24	10	—	20	18	13	6	26
<i>Microseris nutans</i>	16	—	16	8	12	20	7	13	15	7	22
<i>Microsteris gracilis</i>	10	7	8	8	2	3	8	5	—	10	6
<i>Monardella odoratis-</i>											
<i>sima</i>	44	43	56	60	36	43	13	53	45	68	60
<i>Pedicularis semibar-</i>											
<i>bata</i>	4	13	2	8	6	6	8	—	8	10	3
<i>Pinus ponderosa</i> and											
<i>Pinus jeffreyi</i>	100	80	88	86	92	70	88	88	83	87	93
<i>Purshia tridentata</i>	26	33	22	28	26	33	90	38	—	—	3
<i>Senecio integerrimus</i>	26	37	30	34	36	33	12	28	28	55	37
<i>Symphoricarpos vac-</i>											
<i>cinoides</i>	42	53	40	54	32	60	—	8	43	82	82
<i>Viola purpurea</i>	16	16	12	24	24	20	48	25	5	3	10
<i>Wyethia mollis</i>	36	36	32	32	34	17	56	78	2	10	18

100 years. Plant reestablishment is slow, especially in xeric environments (Franklin and Dyrness 1973), yet 40 years is perhaps sufficient time for many species to at least partially recover. This is aided greatly by the heterogeneous nature of the forest, especially the "gap" openings.

TABLE 2. PLANT SPECIES THAT CHARACTERIZE THE TWO COMMUNITIES IN THE FOREST ZONE OF BLACKS MOUNTAIN EXPERIMENTAL FOREST. The numbers in parentheses are the probability of type I error estimated from Analysis of Variance (e.g., $p < 0.01$ for *Purshia tridentata*). Frequency data are estimated from 10 25-m² microplots in each 8-ha macroplot. Species are listed in declining order of overall mean frequency. Species of the Family Poaceae are not included. *Pinus ponderosa*, *Pinus jeffreyi*, and *Ceanothus prostratus* are common in both communities and therefore not listed. ¹ Elevation 1700–1830, m, 10 macroplots sampled. ² Elevation 1800–1950 m, 16 macroplots sampled. ³ Not present on plots in other community. ⁴ More frequent at lower elevations.

Community	
<i>Pinus ponderosa</i> / <i>Purshia tridentata</i> (PIPO/PUTR) ¹	<i>Pinus ponderosa</i> / <i>Symphoricarpos vaccinioides</i> (PIPO/SYVA) ²
<i>Purshia tridentata</i> (<0.01)	<i>Abies concolor</i> (<0.01)
<i>Wyethia mollis</i> (<0.01)	<i>Symphoricarpos vaccinioides</i> (0.06)
<i>Viola purpurea</i> (<0.01)	<i>Monardella odoratissima</i> (<0.01)
<i>Artemisia tridentata</i> ³	<i>Senecio integerrimus</i> (0.04)
<i>Chrysothamnus nauseosus</i> (<0.01)	<i>Arabis holboellii</i> (<0.01)
<i>Collinsia torreyi</i> (0.12) ⁴	<i>Calocedrus decurrens</i> (<0.01)
<i>Achillea millefolium</i> ³	<i>Collinsia torreyi</i> (0.12)
<i>Cercocarpus ledifolius</i> ³	<i>Hieraceum albiflorum</i> (0.06)
	<i>Arctostaphylos patula</i> (0.06)
	<i>Eriophyllum lanatum</i> (0.08)
	<i>Ceanothus velutinus</i> (<0.01)

The results of this study, however, do not imply that timber harvest has no effect on the plant community 40 years after logging in the eastside pine type. Differences in vegetation structure were apparent between the control and more heavily-cut units (e.g., more large snags in the control). The results merely state that long-term effects of timber harvest were not observed in frequency or presence data.

Greater ground disturbance in the CC treatment may have reduced populations of *Ceanothus prostratus* (a prostrate shrub). Table 1 shows that several other species were absent on plots in the CC and IS treatments, or had higher or lower frequencies in the CC treatment; more than three replications of these treatments, and perhaps more than 10 microplots in each unit (replication) were probably necessary to confirm significance.

I estimated that there were 110 to 140 plant species in the forested zone. The total observable flora was noticeably greater during the first summer (1983) following record precipitation, and richness of the flora was probably greater than during a year of average precipitation.

Elevation appeared to be the single most important environmental variable, with a change of as little as 60 m influencing species pres-

ence. Higher frequency of grasses at lower elevations was probably due to decreased canopy cover and increased light filtration in the lower elevation pine forest. Precipitation and soil moisture appeared to increase with elevation. Measurement of these physical influences, as well as aspect and other soil characteristics, is needed to identify which of them may have also contributed to differences in plant communities associated with elevation.

ACKNOWLEDGMENTS

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ANNOUNCEMENT

NEW PUBLICATIONS

GABRIELSON, P. W., R. F. SCAGEL, and T. B. WIDDOWSON, Keys to the benthic marine algae of British Columbia, northern Washington and southeast Alaska, *Phycological Contribution*, no. 2, pp. i-iii, 1-197, Mar 1987, ISSN 0831-4861, ISBN 0-88865-461-8, Can \$6.50 (from R. F. Scagel, Dept. Botany, Univ. of British Columbia, 3529-6270 University Blvd., Vancouver, BC V6T 2B1). [Reproduced from camera-ready copy. For the related "A synopsis of the benthic marine algae of British Columbia, northern Washington and southeast Alaska," *PC*, no. 1, see review by I. A. Abbott, *Taxon* 36:670-671.]

GONZÁLEZ VILLARREAL, L. M., *Contribución al conocimiento del genero Quercus (Fagaceae) en el Estado de Jalisco*, Instituto de Botánica, Universidad de Guadalajara, Apartado 139, Zapopan 45110, Jalisco, 7 Jan 1987, 240, [1] pp., illus., ISBN 968-895-027-0 (paperbound), US \$14.00. [The first volume in *Colección flora de Jalisco*—editorship not indicated. Treatment of the species of *Quercus*, with maps for species, glossary, lists of exsiccatae.]

NOTES

REPORT ON THE XIV INTERNATIONAL BOTANICAL CONGRESS.—The XIV International Botanical Congress was held in West Berlin during the period 20 July through 1 August 1987. There were 14 pre-Congress and 17 post-Congress botanical excursions, extending to the far reaches of Western Europe. Before the Congress, for example, Cherie Wetzel and Larry Heckard joined a small group led by Prof. Arne Strid of the University of Copenhagen in a botanical tour of northern Greece, especially Mount Olympus, while Elizabeth McClintock explored the Canary Islands and William Sanders, a graduate student at Berkeley, collected lichens in Sardinia.

After the Congress, Larry Heckard and I, along with Tom and Mary Fuller and their son Ken, participated in a memorable tour of Czechoslovakia under the guidance of numerous Czech and Slovak botanists, especially Dr. Jan Jeník and Dr. Viera Feráková. Unlike the excursions sponsored by the XII International Botanical Congress in the Soviet Union in 1975, over which the government tourist bureau had rigid control, our program was mainly in the hands of botanists. The politics of the excursion were obvious and amusing. Czechoslovakia comprises two ethnic and political entities, the Czech Socialist Republic with its capital at Prague and the Slovak Socialist Republic with its capital at Bratislava. Everything was counterbalanced. We visited high mountains, lowlands, and limestone outcrops in Bohemia, and high mountains, lowlands, and limestone outcrops in Slovakia. Czechoslovakia has a long and strong botanical tradition; its flora and vegetation have been studied so intensively that only minutiae remain. At times we were exposed to more details than we could absorb, but it was a small price to pay for the privilege of seeing the spectacular plants and scenery of Czechoslovakia and sharing the knowledge and warmth of her wonderfully hospitable people.

The Congress itself was held in the monumental International Congress Centre, conveniently served by Berlin's efficient subway and bus systems. The main building staggers the imagination. It is 300 m long, 80 m wide, and 40 m high. Inside this enormous shell are facilities sufficient to meet the ordinary and special needs of a far larger assemblage than the 4130 botanists and companions of this Congress. Foremost is the main theater, its grand proportions recalling the Radio City Music Hall in New York City. Here is where the opening and closing ceremonies were held. The opening ceremony will be remembered by many of us for the truly outstanding performance by the Westphalian Symphony Orchestra conducted by Walter Gillessen. After an opening fanfare, the ceremony began with vigor and excitement by the playing of Brahms's *Academic Festival Overture*. Brief addresses were given by the President of the Congress (Karl Esser), the Senator for Science and Research for West Berlin (George Turner), the Vice-President of the International Union of Biological Sciences (David Ride), the President of the German Botanical Society (Wilhelm Nultsch), and the Honorary President of the Congress (Frans Stafleu). The ceremony closed with a magnificent concert of German music, running the gamut from Wagner's *Prelude to Die Meistersinger* to Johann Strauss's *Overture to Die Fledermaus*, and including major works by Beethoven, Schumann, and Richard Strauss. Immediately after the opening ceremony, there was a reception, where many members of the California Botanical Society crossed paths and welcomed one another. Besides those already mentioned, I happened to meet Herbert and Irene Baker, Doug Barbie, Tania Beliz, Winslow Briggs, Heidi Dobson, Kent Holsinger, Donald Kaplan, David Keil, Stephanie Mayer, Jeanine Olsen, Ledyard Stebbins, John Thomas, Nancy Vivrette, and Grady Webster.

In addition to the main theater, there are two small theaters with banks of seats that can be retracted to the ceiling, leaving a vast open space. Here is where the

Congress banquet was held, with more than a thousand persons served nearly simultaneously. The smaller meeting rooms varied greatly in their desirability. Topping the list was the roof garden, where the Nomenclature Section met during the week preceding the regular Congress. From the roof of the Congress Centre a panoramic vista of West Berlin and the edge of East Berlin could be obtained, although there was often interference from ominous clouds that brought some rain nearly every day. At the bottom of the list were small meeting spaces cut off from main passageways only by portable partitions. The consensus seemed to be that while nearly everyone was initially turned off by the sheer size and impersonal nature of the Congress Centre, within a few days the dissidents had been converted and looked forward each morning to rejoining their spaceship, which offered comfortable, spacious, and immaculate facilities to accommodate all conceivable daily needs. Next to spaciousness, the most obvious hallmark of the center is the extremely high caliber of materials and workmanship. There are miles of chrome and acres of black synthetic leather. The seats in the main theater are undoubtedly the most comfortable and most expensive I have ever experienced, offering special lumbar support and a reading light.

As for the scientific program, the Congress was very well organized, but there were too many events, even more so than is usually the case. There were 24 general lectures, 224 symposia, 123 poster sessions, 36 special interest meetings, and 25 society meetings. One of my days began with a poster session at 8:30 in the morning and ended at the close of a symposium at 10 in the evening! In my field (phycology), the symposia were generally disappointing, some of the presentations being rehashes of papers given two years earlier at an international phycological congress in Copenhagen. I thought that the contributed papers were more interesting, with some of the best work being presented as posters. Unfortunately, the poster area was extremely crowded. Poster presentations were formalized, being grouped into sessions, each chaired by a moderator. One of the best posters, incidentally, was by Bob Haller of the University of California at Santa Barbara, on the distribution, evolution, and systematics of western American yellow pines.

Despite the fact that most papers dealt with aspects of botany other than those that would be of greatest interest to members of the California Botanical Society, the leadership of the Congress was largely in the hands of taxonomists, reflecting the great strength and importance of the Berlin Botanical Museum and Garden. Its director, Werner Greuter, was chairman of the organizing committee. We were often reminded of the remarkable contributions of a long succession of eminent botanists in Berlin, especially Adolf Engler. During the nomenclature sessions, a magnificent new wing to the botanical museum and library was dedicated. At the closing ceremony, the International Association of Plant Taxonomists awarded the first Engler gold medal to Frans Stafleu in recognition of his enormous contributions to taxonomic botany. The next award of the Engler medal will be made at the XVth Congress in Tokyo in 1993.

What was accomplished at the Congress? As usual the greatest benefit came from personal contacts rather than from formal presentations. The motto of the Congress was "Forests of the World" and attention was focused on the serious plight of our rain forests as well as the equally serious plight of European woodlands. In some parts of Europe a quarter of the trees are dead or dying as a result of atmospheric pollution.

With regard to nomenclature, we were faced with a record number of proposals—334—almost all of which were defeated, either by a preliminary mail vote or by a vote on the floor. Stafleu skillfully but autocratically kept the sessions moving, often so rapidly that confusion ensued. Towards the end of the sessions, fatigue set in, and numerous proposals were referred either to the Editorial Committee or to a series of *ad hoc* committees charged with making their reports prior to the Tokyo Congress.

In December 1987, the Editorial Committee received a compilation of the proposals accepted by the Congress or referred to them for discretionary action, and we met in Berlin during the first week of January to write the new Code. Most changes are of

the nature of clarification or elimination of conflicting rules. The only fundamental change concerns lectotypification. Implicit lectotypification, that is, lectotypification expressed by a taxonomic treatment rather than by an explicit statement, has been outlawed, both in the past and in the future. Thousands of lectotypifications may be affected, especially at the level of species and infraspecific taxa, but the full effect of the new ruling will not be known for many years. I should mention that the official Berlin Code will be in English only, resulting in a prompter, smaller, and less expensive publication compared to previous versions.

Finally, I want to say that all the congressists enjoyed Berlin and Berliners. It is an open-minded, cosmopolitan city, making up for its lack of beauty by its tremendous energy and excitement.—PAUL C. SILVA, Herbarium, Department of Botany, University of California, Berkeley 94720. (Received 9 Nov 1987; revision accepted 22 Feb 1988.)

TYPIFICATION OF *Chaenactis alpina* (ASTERACEAE).—Asa Gray cited no specimens when he described *Chaenactis douglasii* var. *alpina* (Synoptical Fl. N. Amer. 12:341, 1884). The range was given as “Alpine region of the Rocky and Cascade Mountains in Colorado and Wyoming, of the Sierra Nevada, California, and north to Washington Terr.” Stockwell (Contr. Dudley Herb. 3:113, 1940) designated a type, “Alta, Wasatch Mountains, Utah, *M. E. Jones 1232*. (NY)” and stated “Type of A. Gray not known.” There is no indication on the sheet that Gray ever saw this specimen. In GH there are at least five collections prior to 1884 with the name “var. *alpina*” and “Syn. Fl.” on the sheets, including two collections each from California (*Hooker and Gray s.n.* in 1877, *Brewer 1901*) and Colorado (*Parry 55*, *Hall and Harbour 283*) and one collection possibly from Wyoming (not labeled but next to label for *C. douglasii* specimen from Wyoming). These account for Gray’s distribution except for Washington Territory. One sheet contains a fragment collected by Geyer apparently at Spokane Falls but belongs to another species. It can be safely concluded that this material represents some or all of that which Gray used to describe var. *alpina*, and the lectotype must therefore be chosen from among these specimens [Art. T.4.(a), ICBN].

There are two elements represented in the specimens I take to be type material, a glandular or viscid-hirsute element and a tomentose or lanate element. Only the Hall and Harbour specimen fits Gray’s description completely because it is the only specimen with complete rootstocks. It is not, however, the typical variety of Stockwell and others (Harrington, Manual Pl. Colorado 588, 1964; Welsh et al., A Utah Fl. 163, 1987). Another specimen (*Parry 55*), which fits Gray’s protologue except for lacking complete rootstocks, is therefore chosen as the lectotype in order to preserve current usage [Art. T.4.(e), ICBN].

Stockwell’s varieties *rubella* and *leucopsis* appear to be the same taxon. Var. *leucopsis* is taken up here to be consistent with Harrington (Manual Pl. Colorado 588, 1964) and Welsh (Great Basin Naturalist 43:235, 1983). The nomenclature is summarized below.

CHAENACTIS ALPINA (Gray) Jones, Proc. Calif. Acad. Sci. II, 5:699. 1895.—*Chaenactis Douglasii* Hook. & Arn. var. *alpina* Gray, Synoptical Fl. N. Amer. 12:341. 1884.—Lectotype: CO, headwaters of Clear Creek and alpine ridges e. of Middle Park, 1861, *Parry 55* (GH!).

Chaenactis pedicularia Greene, Pittonia 4:98. 1899. Holotype: CO, La Plata Mts., Little Kate Mine, 11,500 ft, *Baker, Earle, and Tracy 536*, 16 Jul 1898 (ND-G; isotype: RM!, US).

Chaenactis pumila Greene, Leaf. Bot. Observ. Crit. 2:221. 1912. Holotype: CA, peak near Sonora Pass, 11,500 ft, *Brewer 1901* (US; isotype: GH!).

CHAENACTIS ALPINA (Gray) Jones var. **LEUCOPSIS** (Greene) Cock. ex. Stockw., Contr. Dudley Herb. 3:114. 1940.—*Chaenactis leucopsis* Greene, Leaf. Bot. Observ.

Crit. 2:221. 1912.—*Chaenactis alpina leucopsis* (Greene) Cock., Univ. Colorado Stud. 11:218. 1915. Holotype: CO, Needle Mountains, 14 Jul 1901, *Whitman Cross 61* (US!).

Chaenactis rubella Greene, Leaf. Bot. Observ. Crit. 2:222. 1912.—*Chaenactis alpina* var. *rubella* (Greene) Stockw., Contr. Dudley Herb. 3:114. 1940. Holotype: north-west Wyoming, 31 Aug 1893, *J. N. Rose 298* (US!).

Variety *alpina* has peduncles and involucre glandular to densely viscid-hirsute with occasionally two to several heads per scape. Variety *leucopsis* has peduncles and involucre tomentose or lanate with usually one head per scape.

Loan of type specimens by US and GH and use of facilities at RM are gratefully acknowledged. Barbara Hellenthal checked for type material at ND-G.—ROBERT D. DORN, Box 1471, Cheyenne, WY 82003. (Received 31 March 1987; revision accepted 30 Nov 1987.)

Chenopodium simplex, AN OLDER NAME FOR *C. gigantospermum* (CHENOPODIACEAE).—Edwin James with the Long Expedition to the Rocky Mountains collected a species of *Chenopodium* in 1820 that John Torrey described in 1827 as a new variety of the European *C. hybridum* L. Torrey thought that it might be a new species. Rafinesque raised it to a species in 1832. These names, *C. hybridum* var. *simplex* Torrey and *C. simplex* (Torrey) Raf., apparently have been largely overlooked ever since. Standley [N. Amer. Flora 21(1):13, 1916] and Wahl (Bartonia 27:30, 1954) do not include them in their treatments, but the Rafinesque combination does appear in Merrill (Index Rafinesquianus, The Arnold Arboretum, p. 118, 1949), and Torrey's variety appears in the Gray Herbarium Index. The holotype is the North American plant that has been called *C. gigantospermum* or *C. hybridum* var. *gigantospermum*. These names must be replaced by *C. simplex* or *C. hybridum* var. *simplex*, respectively.

Bassett and Crompton (Canad. J. Bot. 60:600, 1982) selected a Macoun specimen at CAN for the lectotype of *C. gigantospermum* Aellen. Article T. 4. (c) of the International Code states: "If no holotype was designated by the original author and if syntypes (Art. 7.7) exist, one of them must be chosen as the lectotype." The CAN specimen, therefore, would be a duplicate of the lectotype and the Macoun specimen at US would be the lectotype because Aellen cited only specimens from US (except for one in his own herbarium). Wahl (Bartonia 27:16, 30, 1954), Baronov (Rhodora 66:168–171, 1964), and Bassett and Crompton (Canad. J. Bot. 60:600, 1982) discuss the differences between the European *C. hybridum* and the North American *C. simplex* (as *C. gigantospermum*). The nomenclature is summarized below.

CHENOPODIUM SIMPLEX (Torrey) Raf., Atlantic J. 1:146. 1832.—*Chenopodium hybridum*, ? *simplex* Torrey, Ann. Lyceum Nat. Hist. New York 2:239. 1827.—Holotype: "Near Council Bluff, on the Missouri," *Edwin James s.n.* in 1820 (NY!).

Chenopodium gigantospermum Aellen, Feddes Repert. Spec. Nov. Regni Veg. 26:144. 1929.—*Chenopodium hybridum* var. *gigantospermum* (Aellen) Rouleau, Naturaliste Canad. 71:268. 1944.—Lectotype by Bassett and Crompton (Canad. J. Bot. 60:600, 1982): British Columbia, Vernon, 9 Jul 1889, *Macoun s.n.* (US, photo RM!; isolectotype CAN, photo DAO).

Loan of type material by NY and use of facilities at RM are gratefully acknowledged.—ROBERT D. DORN, Box 1471, Cheyenne, WY 82003. (Received 30 Mar 1987; revision accepted 30 Nov 1987.)

Arabis breweri S. WATS. var. *austinae* (GREENE) ROLL. (CRUCIFERAE)—Ventura Co.: Rose Valley Falls, Sespe Valley, 7 Mar 1947, *Pollard s.n.* (CAS). Monterey Co.: Santa Lucia Range, n. slope of Twin Peak, trail between Goat Camp and Trail Spring

Camp, T21S R4E S34, 1130 m, 2 Feb 1984, *Haller 3600* (UCSB). Colusa Co.: ridge above Red Bridge Camp and confluence of n. and middle forks of Stony Creek, on serpentine, 580–640 m, 16 Apr 1950, *Bacigalupi 3106* (JEPS, UC). Tehama Co.: ca. 10.9 km sw. of Paskenta, on metavolcanic outcrops, T23N R7W sw. $\frac{1}{4}$ S28, 793 m, 25 Apr 1986, *Preston 534* (CAS, DAV). Trinity Co.: dry rocky hillside above Deer Lick Springs Rd., 4.8 km from junction with Hwy. 3, 12 May 1979, *York 271* (HSC). Siskiyou Co.: near Yreka, along Shasta River, 20 Apr 1934, *Eastwood and Howell 1762* (DS, RSA, UC). Shasta Co.: canyon of Low Pass Creek, base of limestone cliffs, 460 m, 30 Jun 1959, *Bacigalupi 7176* (JEPS); n. side of McCloud arm of Lake Shasta, off Gilman Rd., 24 km from U.S. 99, 490 m, 25 Jun 1969, *Heckard 2319* (UC); Shasta-Trinity National Forest, T36N R2W nw. $\frac{1}{4}$ of nw. $\frac{1}{4}$ S32, limestone outcrop, 13 May 1980, *Williams 359* (UC). Plumas Co.: 4.8 km w. of Belden, moist cliffs, 5 Jun 1942, *Heller 16500* (UC).

Previous knowledge. Known from the foothill canyons of Butte Co. and from the canyon of the South Fork of the Yuba River near Washington, Nevada Co. [Howell, Notes on *Arabis* in the Sierra Nevada, *Fremontia* 1(2):13–16, 1973]. Previously, the populations appeared to be confined to volcanic or metavolcanic outcrops.

Significance. The discovery of a disjunct population in Tehama Co. prompted a search for additional locations among specimens of *Arabis breweri* in the major California herbaria. The above collections indicate that var. *austinae* ranges from Ventura Co. north through the Coast Ranges to near the Oregon border, then south into the northern Sierra Nevada. In addition, the list of substrates has increased to include serpentine and limestone. This distribution and substrate preference parallels that of the typical variety, although var. *austinae* generally occurs within the lower range of elevations for *Arabis breweri*.

Arabis breweri var. *austinae* is currently on the watch list of the inventory of California's rare and endangered plants (Smith and York, CNPS Spec. Publ. No. 1, 3rd ed., 1984). This range extension indicates that var. *austinae* is too widespread to be a plant of concern. In addition, the parallel distribution of this variety and the typical variety reinforces the position that var. *austinae* is a weakly segregated taxon. Although var. *austinae* is generally more robust and has larger leaves, flowers, and fruiting pedicels than the typical variety, there were many intermediates among the specimens examined, and populations of var. *austinae* that I have visited have a mixture of robust and typical individuals. The basis for this intrapopulational variation is unknown. On the other hand, the size variation observed between populations clearly has a genetic component. Progeny of robust individuals from a population of var. *austinae* and of typical individuals from a population of var. *breweri* maintained the characteristics of their respective parents when grown together under identical controlled conditions (pers. obs.).

I thank curators of the cited institutions for loans or access to specimens and Rick York for information from the CNPS rare plant file on var. *austinae*. —ROBERT E. PRESTON, Department of Botany, University of California, Davis 95616. (Received 20 Oct 1986; revision accepted 9 Dec 1987.)

NOTEWORTHY COLLECTIONS

CALIFORNIA

Renewed field and herbarium work on the White Mts. of e. CA and w. NV during recent years has revealed the following CA collections of note:

CAREX PARRYANA C. Dewey var. **HALLII** (Olney) Kukenthal (Cyperaceae).—Mono Co.: Inyo Natl. For., White Mts.: subalpine meadow at Deep Springs Cow Camp, 0.65 mi [1.05 km] s. 10° w. of Station Peak, Deep Springs Valley drainage, 9490 ft [2890 m], 13 Aug 1983, *Morefield 1698* (NY); head of e. branch of s. fork of upper Middle Cr., Fishlake Valley drainage, T2S R33E S4, 11,100 ft [3380 m], 23 Aug 1986, *Taylor 8851* (RSA).

Significance. First CA reports of the species and variety, and an extension for both ca. 190 km sw. from the nearest known site in Nye Co., NV.

DRYOPTERIS FILIX-MAS (L.) H. Schott (Aspleniaceae).—Mono Co.: Inyo Natl. For., White Mts., Cottonwood Cr., Fishlake Valley drainage: 1.4 mi [2.3 km] s. 70° e. of Eva Belle Mine site in Granite Meadow, deep vertical crevices in granite, 9850 ft [3000 m], 2 Aug 1984, *Morefield 2446* (NY, RSA); 1.4 mi [2.3 km] n. 65° e. of Eva Belle Mine site in deep granite crevices, 10,080 ft [3070 m], 10 Jul 1984, *Morefield 2320* (NY); 1.5 mi [2.4 km] nnw. of Station Pk. summit at wall meadow, T5S R35E, se. ¼ of Sect. 10, 8900 ft [2710 m], 31 Jul 1987, *Taylor 9189* (RSA, UC).

Previous knowledge. In CA, known only from a single collection (small scrap) in 1882 from Holcomb Valley in the San Bernardino Mts. (*Parish Bros. 1513*, POM).

Significance. Second known station for CA. The nearest known station of this circumboreal species outside CA is the Flagstaff area of n.-cen. AZ, ca. 560 km to the ese.

MALCOLMIA AFRICANA (L.) R. Brown (Brassicaceae).—Inyo Co.: Inyo Natl. For. White Mts. in Deep Springs Valley drainage, 1.8 mi [2.9 km] due n. of Antelope Spgs. in bed of an old mining road, 6450 ft [1970 m], 25 May 1984, *Morefield 1929* (NY). San Bernardino Co.: naturalized around microwave relay station on nw. side of Kelso Mts., ca. 23 mi [37 km] s. of Baker on Kelbaker Road, 4100 ft [1250 m], 26 May 1983, *Barbe 4087* (RSA).

Significance. First CA reports of this introduced weed. Undoubtedly brought in from NV, where it and several other introductions [such as *Halogeton glomeratus* (Steph. ex Bieb.) C. A. Meyer and *Cardaria pubescens* (C. A. Meyer) Jarm.] are spreading largely unchecked.

MENTZELIA REFLEXA Coville (Loasaceae).—Mono Co.: BLM land, White Mts., Owens Valley drainage at mouth of Coldwater Canyon on calcareous shale talus and scree, T5S R33E S26, 5000 ft [1520 m], 28 May 1986, *Morefield 3700 and McCarty* (BRY, NY, RSA, UC, UCR, and others, to be distributed).

Significance. First report for Mono Co., a disjunct extension ca. 100 km nnw. for a plant otherwise endemic to the Death Valley region.

PENSTEMON BARNEBYI N. Holmgren (Scrophulariaceae).—Mono Co.: Inyo Natl. For., White Mts., Fishlake Valley drainage, moist calcareous gravel along Busher Cr. 0.25 mi [0.4 km] w. of the CA border, T3S R35E, ne. ¼ of nw. ¼ of sw. ¼ of Sect. 17, 5910 ft [1800 m], 3 May 1987, *Morefield 4380 and Turner-Jones* (RSA).

Previous knowledge. Segregated from the *P. miser* complex by N. Holmgren (Brit-

tonia 31:226, 1979) as an endemic of e. and cen. NV, known as far w. as Esmeralda Co. (*A. Tiehm* 7705, RSA).

Significance. First CA collection, and an extension 33 km wnw. from the Silver Peak Range in NV. Also collected in the White Mts. farther e. down the same drainage on the NV side (*Morefield* 4014, RSA). This species should be considered rare and endangered in CA. It is rare in the Busher Cr. drainage, where it is reestablishing after a scouring flash flood on 18 Jul 1984. More plants are likely present farther up the drainage into CA. This canyon apparently is open to livestock grazing, though no recent evidence thereof can be seen. In CA, one also should look for *Penstemon barnebyi* just s. of Busher Cr. in the McAfee Cr. and adjacent drainages, where extensive decaying carbonates provide similar habitats.

POA PATTERSONII Vasey (Poaceae).—Mono Co.: Inyo Natl. For., White Mts., Fishlake Valley drainage, n.-facing s. wall of cirque heading the North Fork of Perry Aiken Cr., ca. 1 mi [1.6 km] ese. of White Mountain Pk., T4S R34E, nw.¼ of Sect. 4, 12,000 ft [3660 m], 24 Jul 1987, *Morefield* 4695.1 and *Ross* (RSA, and others to be distributed).

Significance. First report for CA, an extension of at least 320 km sw. from NV and the Rocky Mts. It was growing intimately with *P. lettermannii* Vasey and *P. suksdorfii* (Beal) Vasey ex Piper, with the latter of which it appears to hybridize, and for both of which it easily can be mistaken in the field.

POTENTILLA CONCINNA J. Richardson var. **DIVISA** Rydberg (Rosaceae).—Mono Co.: Inyo Natl. For., White Mts., Fishlake Valley drainage, protected granitic grus on the ridge ne. of Tres Plumas Meadow, 1.3 mi [2.1 km] s. 55° e. of Tres Plumas benchmark 11,107, 10,400 ft [3170 m], 3 Jul 1984, *Morefield* 2239 (NY, RSA).

Significance. First CA report for the species and variety, and an extension for both ca. 150 km sw. from NV.

RIBES VELUTINUM Greene var. **GOODDINGII** (Peck) C. L. Hitchc. (Grossulariaceae).—Mono Co.: Inyo Natl. For., White Mts., Owens Valley drainage, steep protected marble talus at the mouth of Pellisier Cr., T3S R33E S5, 5900 ft [1800 m], 19 Apr 1986, *Morefield* 3453 and *McCarty* (BRY, GH, MO, NY, RSA, UC, and others). Siskiyou Co.: Klamath Mts. 0.6 mi [1.0 km] n. of Callahan, 50 yds from road in a dry gulch, 3400 ft [1040 m], 28 Jun 1955, *Barbe* 018 (RSA); Lava Beds Natl. Mon. near Fleener Chimneys, ca. 5000 ft [1520 m], 3 Sep 1969, *Thorne et al.* 39015 (RSA); dry hillside along Klamath R. between Shovel Cr. and Fall Cr., ca. 2700 ft [820 m], 15 May 1898, *Applegate* 2126 (RSA).

Significance. First CA reports of this taxon, extending its range ca. 600 km s. from Malheur Co., OR.

SENECIO PATTERSONENSIS Hoover (Asteraceae).—Mono Co.: Inyo Natl. For., White Mts., Fishlake Valley drainage, s.-facing n. wall of cirque heading the North Fork of Perry Aiken Cr., ca. 1 mi (1.6 km) ene. of White Mountain Pk., T3S R34E, se.¼ Sect. 32, 12,200 ft [3720 m], 25 Jul 1987, *Morefield* 4703 and *Ross* (RSA, and others to be distributed).

Previous knowledge. Endemic to the Sweetwater Mts. and adjacent Sierra Nevada (Hoover, Leaf. W. Bot. 3:256, 1943 and 5:60, 1947), and reported as rare from the Wassuk Range of w. NV (Bell and Johnson, *Madroño* 27:30, 1980).

Significance. Disjunct extension ca. 120 km se. for this rare *Senecio*.

STYLOCLINE PSILOCARPHOIDES Peck (Asteraceae).—Representative collections: Inyo Co.: Inyo Natl. For., White Mts., Owens Valley drainage, n. wall of canyon 4 mi [6.4 km] ese. of Laws, T6S R34E S31, 5650 ft [1720 m], 11 Apr 1986, *Morefield* 3389.1 and *McCarty* (RSA and others to be distributed); Panamint Mts.: Pleasant Canyon, 7400 ft [2260 m], 10 May 1906, *Hall and Chandler* 6957 (ARIZ, JEPS, POM, UC,

mixed with and det. as *S. micropoides* A. Gray); Surprise Canyon, 1625 m, 15 Apr 1891, *Coville and Funston 640* (US, det. as *S. micropoides*). Los Angeles Co.: San Gabriel Mts., Mojave Desert slope, ¼ mi [0.4 km] n. of Bob's Gap, 3.5 mi [5.6 km] s. of Llano, n. slope of Holcomb Ridge, ca. 3850 ft [1170 m], 25 Apr 1973, *Thorne 43384 and Wallace* (RSA, det. as *Filago depressa* A. Gray). San Bernardino Co.: Salt Wells Valley, 0.8 mi [1.3 km] w. of CA hwy. 178, 8 air mi [13 km] e. of Ridgecrest, T26S R41E S35, 2300 ft [700 m], 12 Apr 1974, *Holmgren 7749 and Holmgren* (BRY, NY, WTU, det. as *Filago arizonica* A. Gray). Morefield thanks the curators of the herbaria above for loans of material in their care.

Previous knowledge. Widespread in se. OR, sw. ID, w. and s. NV, and sw. UT.

Significance. First reports for CA, where it is frequent throughout the Mojave desert, having passed previously for several other taxa. Use Abrams and Ferris, *Ill. Fl. Pacific States IV*, 1960, to distinguish these and all CA taxa of subtribe Filagininae.

TRIFOLIUM DEDECKERAE J. Gillett (Fabaceae).—Mono Co.: Inyo Natl. For., White Mts., Fishlake Valley drainage, 1.5 mi [2.4 km] nnw. of Station Pk. summit at wall meadow, T5S R35E, se. ¼ of Sect. 10, 8900 ft [2710 m], 31 Jul 1987, *Taylor 9190* (RSA, UC). Inyo Co.: Inyo Natl. For., White Mts., Deep Springs Valley drainage, 3.2 mi [5.1 km] s. 40° e. of Sage Hen Pk. just below Dead Horse Meadow, ne.-sloping granite crevices above Crooked Cr., 7700 ft [2350 m], 26 Jun 1984, *Morefield 2191* (ASC, MICH, MNA, NY, RENO, RSA, UNLV, VDB).

Previous knowledge. Known from one site in Wyman Canyon of the White Mts., and from 6 or 7 isolated sites in the Sierra Nevada farther s.

Significance. First record for Mono Co., an extension 14 km nnw. from Wyman Canyon.—JAMES D. MOREFIELD, Rancho Santa Ana Botanic Garden, 1500 N. College Ave., Claremont, CA 91711-3101; and DEAN WM. TAYLOR, Biosystems Analysis Inc., 303 Potrero St. Suite 29-203, Santa Cruz, CA 95060. (Received 10 Jul 1987; revision accepted 10 Nov 1987.)

NEVADA

ELATINE CALIFORNICA A. Gray (Elatinaceae).—Washoe Co., Pilgrim Lake at the California state line on the Buckhorn Rd. from Duck Flat to Ravendale, T35N R18E S29, ca. 1828 m, 14 Aug 1984, *Tiehm and Schoolcraft 9241* (CAS, NSMC, NY). Locally common on mud flats at the edge of the lake.

Significance. First record for Nevada. Previously known from northern Mexico n. to WA and e. to OR, MT, and UT.

ERYNGIUM ALISMAEFOLIUM E. L. Greene (Apiaceae).—Washoe Co., center of Macy Flat, T47N R21E S32, 1759 m, 22 Jul 1986, *Schoolcraft 1660* (NY), Rye Creek Reservoir, T46N R22E S6, 1654 m, 22 Jul 1986, *Schoolcraft 1661* (UC). Growing on seasonally inundated flats with *Artemisia cana* and near the edge of a reservoir.

Significance. First records for Nevada. Previously known from n. CA to OR and ID.

HACKELIA CUSICKII (Piper) A. Brand (Boraginaceae).—Washoe Co., near California state line at s. end of the Coppersmith Hills, T37N R18E S29, 1889 m, 23 Jun 1986, *Schoolcraft 1636* (NY). Growing under *Juniperus*.

Significance. First record for Nevada. Previously known from Crook and Harney cos. OR s. to Lassen and Siskiyou cos. CA.

LATHYRUS LAETIVIRENS E. L. Greene ex Rydb. (Fabaceae).—Lincoln Co., Clover Mts., Sawmill Canyon, 4 road mi ssw. of the Ella Mt. rd. from Caliente, T5S R67E, 1828 m, 14 May 1987, *Tiehm and Williams 11010* (CAS, NY, RM, RSA). Growing with *Pinus* on talus slopes of rhyolitic rock.

Significance. First record for Nevada. Previously known from n. AZ, s. UT, and w. CO.

OREGON

CRYPTANTHA MICRANTHA (Torr.) I. M. Johnston (Boraginaceae).—Harney Co., Pueblo Valley, 2.6 road mi n. of the state line on highway from Denio to Field and Burns, then 1.6 road mi ne. along a fence line road, T41S R35E S10, 1274 m, 22 May 1987, *Tiehm 11059* (CAS, NY, ORE, OSC, RSA). Growing with *Sarcobatus* in areas of sand on the valley floor.

Significance. First record for Oregon. Previously known from s. CA n. through w. NV to Humboldt Co.

ERIOGONUM BRACHYANTHUM Coville (Polygonaceae).—Harney Co., Pueblo Valley, 0.7 road mi n. of the state line at Denio then 1.8 road mi e. on a rural road, T41S R35E S22, 1274 m, 4 Aug 1987, *Tiehm 11499* (CAS, MARY, NY, ORE, OSC, RSA). Growing with *Sarcobatus* on sand dunes on the valley floor.

Significance. First record for Oregon. Previously known from s. CA n. through w. NV to Humboldt Co.—ARNOLD TIEHM, New York Botanical Garden, Bronx 10458; and GARY SCHOOLCRAFT, BLM, 2545 Riverside, Susanville, CA 96130. (Received 27 Oct 1987; accepted 7 Dec 1987.)

REVIEWS

The Plant-Book: A Portable Dictionary of the Higher Plants. By D. J. MABBERLEY [further subtitle—*Utilising Cronquist's An Integrated System of Classification of Flowering Plants (1981) and Current Botanical Literature, Arranged Largely on the Principles of Editions 1–6 (1896/97–1931) of Willis's A Dictionary of the Flowering Plants and Ferns*], Cambridge University Press, Trumpington St., Cambridge CB2 1RP, England, 1987, xii, 706 pp., ISBN 0-521-34060-8 (hardbound). \$34.50.

Although Mabberley's work is not specifically on Western North American botany, it seems worthy of notice in *Madroño* because it lists almost all the taxa of the region. The book is essentially the real seventh edition of J. C. Willis's *A Dictionary of the Flowering Plants and Ferns* (6 eds. 1897–1931). As is well known, when H. K. Airy Shaw revised Willis's *Dictionary* in 1966 and 1973 (as the 7th and 8th eds. of Willis), to save space he dispensed with much of the general information, for example, common names, definitions of botanical terms, and most of the accounts of economic products and ornamental plants, and in effect turned the work into a nomenclatural dictionary that has, of course, proven to be indispensable. In 1974 F. N. Howes's *A Dictionary of Useful and Everyday Plants and Their Common Names* appeared. This was based on the information expurgated from the 6th, 1931 edition of Willis. Mabberley thoroughly updated this Willis in a comparable-size work that "attempts to present all currently accepted generic and family names and commonly used English names" of extant vascular plants. Economically important plants get very good treatment, for instance, 55 lines for *Eucalyptus*. Most of the families get attention, although there are likely to be omissions for some monotypic or trivial families. Many references are included. Unfortunately, it was not feasible to include a glossary of technical terms, as did Willis (1931). Back matter includes a synopsis of Cronquist's classification system for angiosperms, a bibliography, and lists of abbreviations, including an excellent 46-page list of names of authors. Overall, this is an incredibly valuable effort and should prove to be one of the most useful books published in recent years.—RUDOLF SCHMID, Department of Botany, University of California, Berkeley 94720.

Annotated Checklist of Vascular Plants of Grand Canyon National Park 1987. By BARBARA G. PHILLIPS, ARTHUR M. PHILLIPS, III, and MARILYN ANN SCHMIDT BERNZOTT. 79 pp., soft cover. Grand Canyon Natural History Association, P.O. Box 399, Grand Canyon, AZ 86023-0399; Monograph No. 7. 1987. \$10.00 (free to researchers making request on official letterhead).

This is an attractive and well-organized book on the botany of the Grand Canyon. The large format ($8\frac{1}{2} \times 11$ inches) and the small, but easy to read, font allow for much information per page. The first checklist of the Canyon, by Patraw in 1932, listed only 450 species of plants. The last checklist, by McDougall in 1947, listed about 900. The present effort includes some 1400 species. The authors point out that much of the Inner Canyon remains botanically unexplored and that the list will continue to grow.

Part One includes a brief survey of the history of botany in the Canyon and sources of information (recent field work, herbaria, publications) for the checklist, followed by an in-depth discussion of the vegetation and climate of the North Rim, South Rim, and Inner Canyon. This is followed by a discussion of Grand Canyon paleoecology. This section includes the only figure, an interesting drawing that compares Late Pleistocene and present-day vegetation in the vicinity of Rampart Cave.

Part Two is the annotated checklist. In preparing the list the authors used, but did not blindly adhere to, Lehr (1978, *A Catalogue of the Arizona Flora*) and the subsequent supplements (Lehr and Pinkava, 1980 and 1982, *J. Ariz.-Nev. Acad. Sci.*). All taxa are alphabetically arranged within major groups: ferns and fern allies, gymnosperms, monocotyledons, and dicotyledons. Annotation information for each species and infraspecific taxon includes "scientific authority" (=author of scientific name), common name, growth form, notation if exotic or introduced, habitat, and (within the Park) distribution, elevational range, and flowering and fruiting times. Only six easy-to-remember abbreviations are used (CRM = Colorado River Mile, a standard designation; L = left side of river; etc.), making the annotations very readable.

A useful appendix cross-references the nomenclature from Kearney and Peebles (1960, *Arizona Flora*) to that used in the checklist. A rather generalized map of important localities within the Park is printed on the end covers.

I find it difficult to find faults with this well-written book. My only major criticism is that a large percentage of the species are cited as "reported from" one or more particular localities: "*Fimbristylis thermalis* Wats. Perennial herb; reported only from foot of Bright Angel Trail, Inner Canyon. 2400 feet. Fl. & Fr. Aug. (Thornber 8237)." Initially I was confused by the use of the phrase "reported from" in combination with a specimen citation because neither an herbarium nor a publication is cited. The authors do not make clear that in each of these cases they did not examine a specimen but instead found the species, and sometimes a specimen, cited in a published or unpublished list for the Park (A. Phillips, pers. comm.).

Another minor peculiarity of the list is that the epithets *johnsoni*, *watsoni*, *eatonii*, etc. are sometimes corrected according to the International Code of Botanical Nomenclature (Art. 73.10: *johnsonii*, *watsonii*, *eatonii*, etc.) but often they are not. After much searching for typographical errors I was able to find only one (p. 67, correct spelling: *Forsellesia nevadensis*). In the bibliography McClintock's single reference (1952) occurs between McDougall 1964 and McDougall 1973. I include these corrigenda for the serious user; this book's errors are rare and do not significantly detract from its high quality.

This checklist is indicative of the remarkable diversity of the Grand Canyon. Any student of the plants of Arizona, particularly northern Arizona, will find Part One to be interesting reading and Part Two a useful reference on the plants of this vast and largely inaccessible region of the state.—BRUCE D. PARFITT, Department of Botany, Arizona State University, Tempe 85287-1601.

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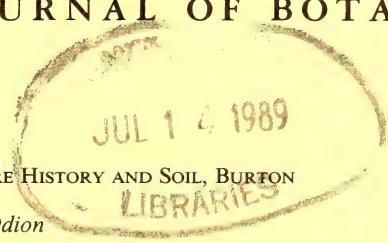
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MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

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COMPOSITION OF MARITIME CHAPARRAL RELATED TO FIRE HISTORY AND SOIL, BURTON MESA, SANTA BARBARA COUNTY, CALIFORNIA

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ABSTRACT

Maritime chaparral of Burton Mesa, California was sampled to determine trends in species richness, vegetation structure, and composition after fire. Species cover is estimated in 75 100 m² plots distributed among 28 sites that range from 1 to 50+ years since burning. Twenty-eight plots were located under coast live oaks (*Quercus agrifolia*) that are scattered among the chaparral shrubs, and 47 plots located in surrounding chaparral. Vegetation data were analyzed and related to stand age, soil depth, texture, and pH, and distance from the coast using Detrended Correspondence Analysis (DCA) and Canonical Correlation Analysis (CCA).

Species richness is highest during the first 3–5 years after fire, but is more strongly related to total evergreen shrub cover than stand age. Physiognomic trends in chaparral samples are similar to those reported for other chaparral types. Oak understories differ from chaparral in that annuals decline more rapidly during the first 10 years after fire, and subshrubs are not as important. The composition of the herb layer under oaks is associated with stand age and distance from the coast. In chaparral samples, composition of perennials is related to stand age, distance from the coast, depth to a subsoil pan, soil pH, and soil texture. The composition of annuals and biennials in chaparral is related to stand age, canopy coverage by evergreen shrubs, depth to a subsoil pan, and distance from coast.

After fire in California chaparral, regeneration of shrubs by sprouts and seeds produces a rapid return of the vegetation present before the burn (e.g., Sampson 1944, Horton and Kraebel 1955, Sweeney 1956, Hanes 1971, Keeley et al. 1981; reviews in Hanes 1977 and Vogl 1981). A diverse flora of herbs and subshrubs also flourishes for several years after fire, declining or disappearing with closure of the shrub canopy (Christensen and Muller 1975, Hanes 1971, J. Keeley et al. 1985, S. Keeley et al. 1981, Schlesinger et al. 1982). Patterns in post-fire vegetation development vary depending on chaparral composition, fire timing and intensity, and the physical attributes and disturbance history of the site (Keeley and Zedler 1978, Malanson and O'Leary 1985). Most studies of chaparral succession have been located on the steep slopes and shallow soils of the Transverse and Peninsular ranges of California. Although general vegetational trends are known, more research is needed to

understand how physical and biotic factors interact to control local and regional variation in post-burn vegetation recovery.

We have studied post-fire succession in maritime chaparral on Burton Mesa, near Lompoc, California. We chose this area for two reasons. Since 1938, at least 27 fires have occurred in a small area (ca. 4000 ha) of uniform climate, geology, and topography, providing a relatively large sample for analyzing patterns of chaparral development after fire. Moreover, there is a practical reason for analyzing this chaparral community. Burton Mesa supports a rich chaparral flora with many endemic taxa (Ferren et al. 1984). As in other maritime chaparral communities, much acreage has been converted to residential, agricultural, and military uses, and most remaining areas are under development pressure and are experiencing invasion by exotic weeds such as *Carpobrotus edulis* and *Cortaderia jubata* (Griffin 1978, Jacks et al. 1984). Of the approximately 9000 hectares of original upland habitat, we estimate that only 5890 ha of Burton Mesa chaparral existed in 1938 and less than 3500 ha remain today. An understanding of vegetation ecology and regeneration after fire is needed to provide a basis for adequate protection and management of the remainder of this threatened, endemic-rich chaparral. In this paper we describe the modern fire history of Burton Mesa, document the importance of subsoil morphology, distance from the coast and stand age in determining stand composition, and compare post-fire development with that occurring in other chaparral types.

STUDY AREA

Location and climate. Burton Mesa is located north of Lompoc in northern Santa Barbara County (Fig. 1). The western half of Burton Mesa is within Vandenberg Air Force Base.

The local climate is Mediterranean, having a strong maritime influence, cool summers, and mild winters. Over 90% of the 36 cm average annual precipitation falls between November and April. Prevailing winds from the northwest deliver salt spray up to 50 km into the Santa Ynez Valley (Ogden 1975). Coastal fogs, especially prevalent during late spring and summer, greatly reduce potential evapotranspiration. We sampled vegetation during the winter and spring of 1985/86, which were warmer than average (Fig. 2). December and April were relatively dry, but November and March were wet, and total precipitation was near average (Fig. 2).

Geology and soils. Burton Mesa is underlain by marine sedimentary rocks and gravels which are covered with Orcutt sandstone, 0.5 to 40 m of weakly cemented Quaternary aeolian sand (Dibblee 1950, Johnson 1983). The topography comprises level to gently rolling uplands 100 to 120 m above sea level.

In general, topsoil on Burton Mesa is uniformly medium sand.

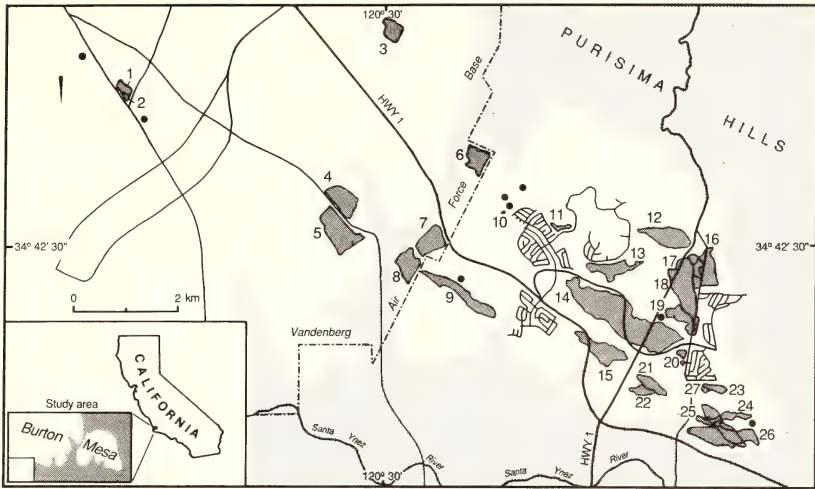


FIG. 1. Map of study area showing approximate extent of Burton Mesa uplands (unshaded) and documented fires occurring between 1938 and 1985 (dark shading). Numbers designate historic fires, dots (●) represent plots in chaparral not burned within the last 50+ years (see Table 2 for explanation).

However, soils vary in depth to bedrock, or to a clay, iron-, or silica-indurated pan, and several soil series are recognizable based on soil depth and subsoil properties, the most widespread being the Marina, Tangair, and Narlon sands (Shipman 1972). The Marina series covers most of the eastern mesa and consists of deep (>1.5 m), excessively drained and infertile loamy sand. Tangair and Narlon sands cover large portions of the central and western mesa. The Tangair series is characterized by one to several meters of nutrient-poor light gray sand over an impermeable or slowly draining subsoil. The sandy layer often contains fresh iron nodules. The Narlon series is similar to the Tangair series but distinguished by a clay subsoil and very poor drainage. In our experience, the color, depth, and drainage characteristics of all three series can vary considerably within Soil Conservation Service mapping units.

Vegetation. Our analysis is restricted to the level uplands of Burton Mesa. The native vegetation is fragmented by roads, residential areas, agriculture, and other developments. Vegetated areas are covered by chaparral shrubs including *Adenostoma fasciculatum* and the local endemics *Arctostaphylos rudis* Jeps. & Wies., *A. purissima* P. V. Wells, *Ceanothus ramulosus* var. *fascicularis* McMin., and *C. impressus* var. *impressus*. Multi-stemmed coast live oaks (*Quercus agrifolia*) 3–6 m in height are interspersed throughout the chaparral, attaining $>20\%$ crown cover in some areas not recently disturbed

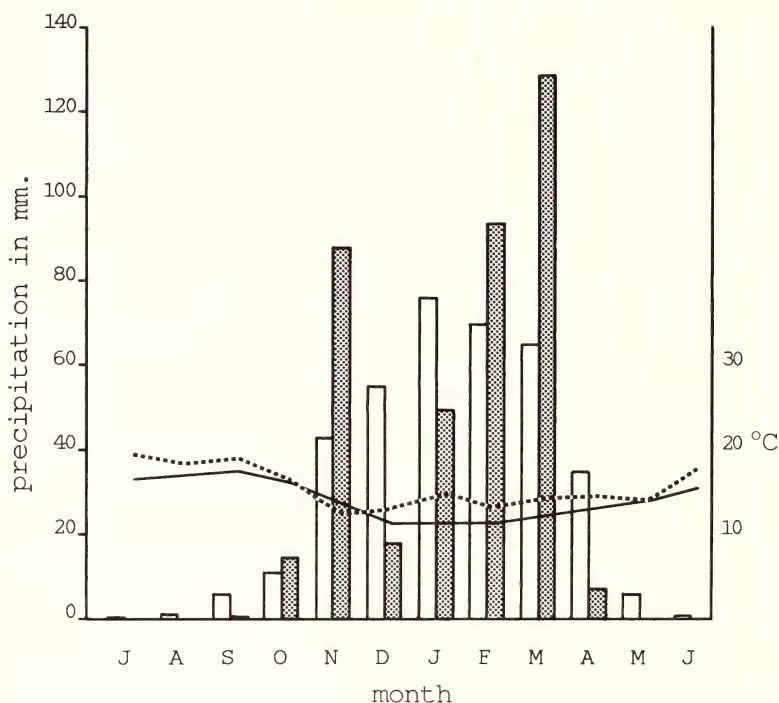


FIG. 2. Climate data for Lompoc, California. Open bars are monthly average precipitation for the period 1951-1985; shaded bars are monthly means for July 1985 to June 1986. Solid line is monthly average temperatures for the period 1951-1985, and the dashed line for July 1985 to June 1986.

by burning or clearing. Annual grassland and coastal sage scrub characterized by *Ericameria ericoides*, *Artemisia californica*, and *Baccharis pilularis* occur on formerly cleared sites and on xeric slopes. Some poorly drained upland sites in the central and western portions of Burton Mesa form seasonal wetlands characterized by native perennial grasses such as *Elymus glaucus* and vernal pool species including *Eryngium armatum*.

The vegetation of Burton Mesa has received little systematic study. Wells (1962) and Cole (1980) have described the strong association of plant species and geology in the region. Ferren et al. (1984) provide a thorough description and floristic analysis of vegetation of La Purisima Mission State Historic Park, at the eastern end of Burton Mesa. Halligan (1973) studied stands of *Artemisia californica* in the park to determine the factors suppressing understory growth in coastal sage scrub, and Ogden (1975) investigated the role of salt aerosols in limiting the local distributions of *Quercus lobata* and *Quercus agrifolia*.

METHODS

Fire history. We reconstructed the fire history of Burton Mesa since 1938 from aerial photography that provided coverage at 5- to 10-year intervals. Past issues of the *Lompoc Record* were studied for references to the date, size, location, and cause of fires. In addition, Santa Barbara County records were checked, and fire department personnel at Vandenberg Air Force Base were interviewed. Burn scars were located on air photos and mapped onto USGS 7½ minute topographic maps using a Bausch and Lomb Zoom Transfer Scope. Burned areas in the chaparral were detectable on air photos for up to 10 years after the fire, allowing almost continuous coverage for the 50-year time period.

Vegetation and soil sampling. To study vegetation development after fire, we sampled level to moderately sloping uplands that had not been grazed or cleared since at least 1945, locating plots away from roads or trails to avoid edge effects. We sampled 47 stands on 33 sites that spanned nearly the entire length of Burton Mesa and ranged in age from 1 to 50+ years. The Braun-Blanquet relevé approach (Mueller-Dombois and Ellenberg 1974) was used to characterize vegetation of a burn. Each burn area was first reconnoitered, and sample plots were subjectively located in large distinctive stands that best represented the post-fire vegetation. Time constraints limited the number of plots to a maximum of four for the most heterogeneous burn sites. Because of limited historical aerial photography for Vandenberg Air Force Base, and also because of apparently lower fire frequency on western Burton Mesa, we sampled the central and eastern portions of Burton Mesa more intensively than western Burton Mesa. We subsequently have discovered that much of the western mesa was cultivated prior to 1938.

The vegetation at most sites included chaparral with scattered coast live oaks. We sampled oak understories and chaparral separately to compare post-fire vegetation development in the two microenvironments. Depending on the size of the burn and the variation in vegetation, we placed one to three sample plots in chaparral (hereafter referred to as "chaparral plots"), and one under oak canopy ("oak plots"), for a total of 47 chaparral plots and 28 oak plots.

Chaparral plots were circular and 100 m², an adequate size based on species-area curves at four sites from 1 to 50+ years. The shape and size of oak plots varied among individual oak canopies, which were sampled in their entirety and which ranged in size from roughly 50 to 150 m². We sampled stands by visually estimating cover (Braun-Blanquet cover classes) of all vascular plant species in the plots. The same observers, at least two and usually three of us, estimated species cover for all samples, helping to reduce effects of observer bias on species cover estimates (Gotfryd and Hansell 1985). We visited all

plots in 1986 in early, mid-, and late spring (22 March through 20 May), and in August, as needed, so that their entire flora and the maximum cover for each species could be observed.

Oak canopy cover in a stand was measured photogrammetrically by centering a 10×10 grid on the stand in 1:24,000 1983 aerial photographs. The grid corresponded to 120×120 m on the ground. The fraction of each 12×12 m grid cell covered by oak canopy was visually estimated and values summed to obtain the percent oak cover for the stand.

For each chaparral plot we used a 2.5 cm diameter soil probe to observe soil texture, color, and stratigraphy and to measure the depth (up to 1.8 m) to a sub-surface pan or to bedrock. For all plots, soil samples composited from the top 20–30 cm of topsoil were dry-sieved in the lab to determine particle size distribution. Soil pH in both water and a KCl solution was measured. Values reported here are for measurements made in water.

Nomenclature follows Munz (1959, 1968) except where author is noted. Voucher specimens are deposited at UCSB and SBBG.

Data analysis. We analyzed species cover data using Detrended Correspondence Analysis (DCA) (Hill and Gauch 1980), canonical correlation analysis, and direct ordination. DCA is an indirect ordination method for representing the relative similarity of samples or species along a few principal axes of variation, which can be studied for their relationship to environmental variables. The method is especially useful for detecting linear or unimodal gaussian relationships between species and environmental gradients. Thus the method works best for sampling vegetation along one to several environmental gradients within a narrow range of environmental variation over which species responses may exhibit single optima (Austin 1976, Noy-Meir and Whittaker 1977). We restricted our sampling to chaparral on level uplands of a single geologic substrate in an effort to produce data that would be amenable to indirect ordination analysis. We performed separate ordinations for four species groups, because we found that the stratification produced clearer relationships between ordination scores and environmental variables. These groups included annual and biennial species in chaparral plots, perennial species in chaparral plots, annual and biennial species in oak plots, and perennial species in oak plots.

Ordination results can be sensitive to data quality, data transformations, weighting of rare species, and standardization and normalization procedures (Noy-Meir et al. 1975). We tested the stability of DCA ordinations obtained using species presence-absence versus cover class data, and those with and without downweighting of rare species. Downweighting in the DECORANA program was accomplished by reducing species abundance values in proportion to their

frequencies of occurrence, for species with frequencies less than 20% of the most frequent species (Hill 1979). The ordinations were relatively insensitive to the weighting of rare species. However, ordination scores were sensitive to data quality, with poor agreement between results obtained for presence-absence data versus cover class data. The ordinations based on perennial species cover provided a better reconstruction of plot similarity than the presence-absence ordinations. This is expected, given the importance of dominant canopy species in chaparral stands. On the other hand, the ordinations based on the presence or absence of annual species gave more interpretable axes than those based on cover data. Annual species rarely exceeded 1–5% ground cover in a plot; their cover varied over the season and was typically patchier than perennial cover. The cover estimates for annuals were thus not as meaningful nor reliable as those for perennials, and species presence was a more appropriate measure. Here we present plot ordination results based on perennial cover and on annual species presence-absence data, with no downweighting of rare species.

Variables analyzed for their correlation with the first and second DCA axes included years since burning, depth of soil over a clay or iron pan or over bedrock, distance from the coast along the predominant wind direction (northwest), soil pH, and percent fine fraction (<0.1 mm) in the upper 30 cm of the soil. Also, correlation was measured between sample ordination scores based on herb species composition and total canopy cover of evergreen shrubs.

Some environmental parameters are highly correlated, making it difficult to interpret correlations between ordination axes and individual environmental variables. Soil depth and soil fine fraction are both significantly negatively correlated with distance from the coast (Table 1). Soil fine fraction is positively correlated with soil pH, and evergreen shrub canopy cover is positively associated with stand age. To help account for the interrelationships between environmental variables, we performed canonical correlation analyses using the first and second axis scores for plot ordinations and selected environmental factors (Dillon and Goldstein 1984). Environmental variables were first standardized to mean 0 and standard deviation of 1. Log transforms of plot age and distance from the coast were used because the transformation increased the linear relationship between these variables and the ordination axes.

Canonical correlation analysis is a generalization of multiple regression analysis that identifies canonical axes that maximize the correlation between two groups of descriptors, in this case DCA axis scores and environmental factors. The technique is applicable only when descriptors are linearly related, limiting its use in ecological analyses (Legendre and Legendre 1983). Some alternative techniques have been developed recently, such as canonical correspondence

TABLE 1. CORRELATION HALF-MATRIX OF ORIGINAL AND TRANSFORMED ENVIRONMENTAL VARIABLES MEASURED FOR EACH CHAPARRAL PLOT (n = 47). Age is years since burning; Canopy is total evergreen shrub cover; Distance is from the coast; Depth is soil depth to consolidated pan or bedrock; Fines is percent fine silt and clay in the upper 30 cm of the soil; pH is soil pH measured in water. 95% significance is indicated by asterisk.

	Age	log(Age)	Canopy	Distance	log(Dist.)	Depth	Fines
log(Age)	0.878*						
Canopy	0.527*	0.687*					
Distance	-0.035	0.171	0.301*				
log(Distance)	-0.054	0.132	0.264	0.944*			
Soil depth	-0.078	0.081	0.205	0.772*	0.751*		
Fines	0.034	-0.055	-0.045	-0.464*	-0.440*	-0.561*	
pH	-0.243	-0.234	-0.214	-0.262	-0.226	-0.243	0.435*

TABLE 2. DATES AND SAMPLE ALLOCATION FOR FIRES OCCURRING ON THE BURTON MESA BETWEEN 1938 AND 1985. Fire numbers correspond to areas in Fig. 1.

Fire	Number of plots	Year of fire
1	1	1984
2	2	1983
3	2	1981
4	3	1981
5	2	1985
6	0	1983
7	4	1982
8	2	1983
9	3	1982
10	1	1976
11	0	ca. 1973
12	4	1967
13	4	1976
14	2	1967
15	4	1962
16	3	1976
17	5	1985
18	1	1972
19	2	1974
20	0	ca. 1973
21	0	ca. 1962
22	0	ca. 1960
23	3	1974
24	4	1974
25	6	1961
26	0	1971
27	0	ca. 1970

analysis (Ter Braak 1987), which use constrained ordination to ensure linear relationships between ordination axes and environmental factors. We tested several constrained ordination methods, including detrended canonical correspondence analysis and redundancy analysis (Ter Braak 1987), and obtained results similar to those obtained using canonical correlation analysis. We present the latter results here because canonical correlation analysis is a more widely known method.

RESULTS

Fire history analysis. We located 27 fires larger than 1 ha that occurred between 1938 and 1986 (Fig. 1, Table 2). Several other large fires occurred on VAFB during the period, but these could not be accurately mapped due to inaccessible or incomplete photo coverage and records for the base. Most fires spread in the direction of prevailing northwesterly winds and were extinguished at or arrested by roads, fields, or fuel breaks. All 27 fires were started by humans;

the eight fires on Vandenberg AFB were controlled burns, whereas the others were either accidental or arson fires. The *Lompoc Record* reported only one possibly lightning-caused fire in the region during this period. That fire originated on Tranquillon Mountain, a 650 m peak 15 km s. of Burton Mesa, but did not reach the mesa.

Flora and physiognomy. We encountered 41 families, 110 genera and 152 species of vascular plants in the sample plots (Appendix 1). The largest families include Asteraceae (36 species), Poaceae (16), and Scrophulariaceae (8). Two species, *Arctostaphylos rudis* and *A. purissima*, are endemic to the Burton Mesa; five others are endemic subspecies or varieties, including *Ceanothus ramulosus* var. *fascicularis*, *C. impressus* var. *impressus*, *Mimulus aurantiacus* subsp. *lompocensis*, *Amsinckia spectabilis* var. *microcarpa*, and *Erysimum suffrutescens* var. *lompocense*. Thirty species are exotic.

The flora includes one tree, 17 shrubs, 17 subshrubs, 31 perennial herbs, and 86 annual or biennial species. The most frequent shrubs are *Adenostoma fasciculatum* and *Ceanothus ramulosus* var. *fascicularis*, whereas the most frequent subshrubs are *Horkelia cuneata* and *Lotus scoparius*. *Melica imperfecta* is the most frequent perennial herb, and *Camissonia micrantha* and *Vulpia octoflora* the most frequent annuals. Of the annuals and biennials 39 of 86 species (45%) occur in three or fewer plots, and 18 species (21%) occur in only one plot. Twelve of 31 perennial herb species (39%) occur in three or fewer plots, and, of these, 10 (32%) occur only once. In contrast, only one of 35 (3%) woody perennial species (*Solanum douglasii*) occurs in fewer than three plots.

In general, species richness declines during the first 15–20 years after burning, but there is considerable variation in richness between plots of the same age (Fig. 3). Recently-burned chaparral plots have consistently high richness; $\bar{S} = 36$ species for 14 plots <10 years of age. Species richness averages 20 in 35 plots older than 20 years, and does not differ significantly between plots 20–30 years of age and those at least 50 years old. Species richness is generally lower in oak plots, and for the first 25 years after fire, species richness appears to decline more rapidly ($p < 0.10$) in oak plots than in chaparral plots. The slope of the regression line relating species richness to plot age is -0.93 for chaparral ($n = 38$, s.d. = 0.17) and -1.26 under oak canopies ($n = 26$, s.d. = 0.17). When all chaparral plots are considered, species richness is negatively correlated with total evergreen shrub cover ($r = -0.76$, $p < 0.01$), less so with years since burning ($r = -0.56$, $p < 0.01$) or the logarithm of years since burning ($r = -0.65$, $p < 0.01$). We tested for possible effects of other environmental variables on species richness by including them with plot age and shrub cover in a stepwise multiple regression analysis. Neither soil variables nor distance from the coast were significantly

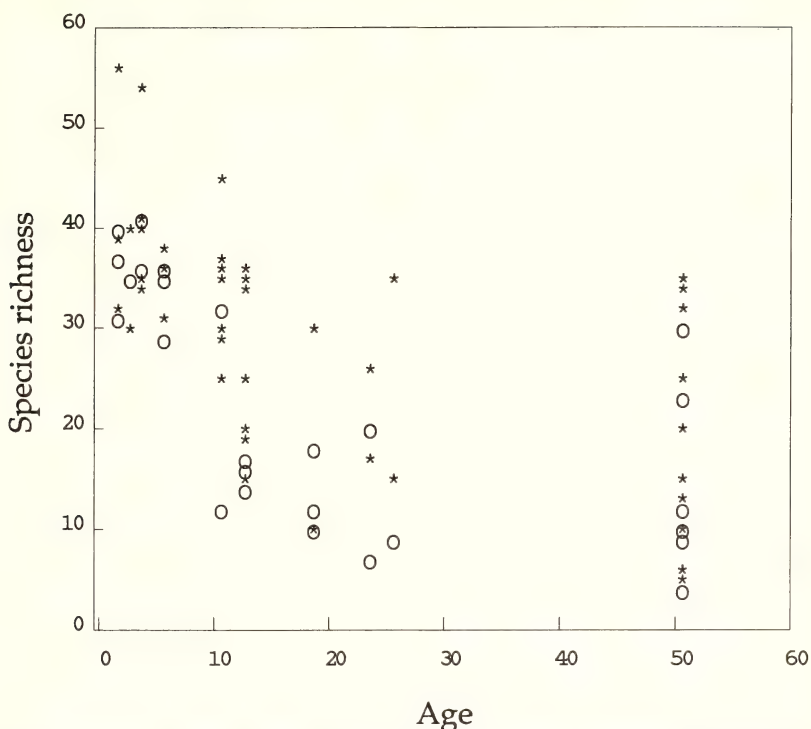


FIG. 3. Species richness versus years since fire for plots in chaparral (*) and oak understories (O).

correlated with species richness, and none of them significantly improved regression model r^2 over the model based solely on total shrub cover.

The decline in species richness in chaparral plots is due to proportional declines in number of species of all growth forms, whereas under oaks it is due mainly to a reduction in the number of annual species (Table 3). The decline in understory richness under oaks, unlike that in the chaparral plots, is not accompanied by a decline in understory cover. The understories of oak plots in the older age classes varied from a cover of 25–50% *Toxicodendron diversilobum* to less than 5% cover of one to several perennial species. Trees with low understory richness and cover were frequently associated with nests of the wood rat (*Neotoma* sp.).

For chaparral plots, physiognomic trends during recovery from fire are similar to those described for other chaparral communities (Table 3). Herbs and subshrubs account for most of the cover in chaparral plots less than 5 years old. Dominant herb species include *Vulpia octoflora*, *Chorizanthe diffusa*, *Camissonia micrantha*, *Cras-*

TABLE 3. GROWTH FORM DISTRIBUTIONS FOR BURTON MESA CHAPARRAL AND OTHER SELECTED CALIFORNIA CHAPARRAL TYPES. For Burton Mesa plots, sample size in each age class is indicated (n). Representation by different growth forms is expressed as percent of total species (%S) or as percent of ground covered (%C). 1—Estimated from Keeley et al. (1981), Fig. 2, Table 1. 2—Shmida and Whittaker (1981), Table 3. 3—Naveh and Whittaker (1979), Table 4. 4—Mooney et al. (1977), Table 5.1.

Location	Age	n	Total species	Annual		Per. herb		Subshrub		Shrub	
				%S	%C	%S	%C	%S	%C	%S	%C
Burton Mesa shrub plots	1-2	6	96	52	12	16	6	15	14	17	10
	3-5	9	89	54	4	19	<1	12	37	16	27
	10-12	14	91	52	2	16	1	15	12	16	64
	18-25	8	59	49	1	15	0	15	7	20	87
	50+	10	73	48	2	18	1	14	2	21	64
Burton Mesa oak plots	1-2	4	80	61	11	10	2	14	<1	15	4
	3-5	5	74	50	37	15	1	18	8	18	24
	10-12	6	49	39	11	16	2	20	1	24	29
	18-25	6	32	22	<1	19	1	25	7	34	12
	50+	7	29	21	<1	28	1	17	<1	34	23
Chaparral, San Diego Co. ¹	1-2				18		1		9		9
	3-5				18		2		15		41
	9				19		3		0		58
	16				2		3		3		65
<i>Adenostoma</i> chaparral ²	mature		29	66		10		7		14	
<i>Ceanothus</i> chaparral ³	mature			46		19		10		25	
Chaparral, San Diego Co. ⁴	mature		44	13		30		16		41	

sula erecta, *Filago californica*, and *Cryptantha clevelandii*. Cover of subshrubs such as *Helianthemum scoparium*, *Lotus scoparius*, and *Eriophyllum confertiflorum* peaks 3–5 years after fire, after which shrub cover dominates. Total cover is not as high in the oldest plots as in the 18–25 year range, due mainly to *Ceanothus ramulosus* mortality. Dead individuals of this species are common in chaparral over 20 years old on deep soils.

Coast live oaks attain highest density and canopy cover on sites with no recent fires, particularly on deep sands in the eastern portion of the mesa. Oak canopy cover is significantly related to time since last fire ($r = 0.67$, $n = 49$, $p < 0.001$), although cover ranges widely on sites of similar age depending on microtopography, soil, coastal influence, and fire intensity.

The physiognomic trend in plant cover under oaks differs from that under the chaparral shrubs, in that annuals continue to dominate plant cover for 3–5 years after fire, and subshrubs like *Helianthemum scoparium* and *Lotus scoparius* are never a major component of the understory (Table 3).

Vegetation ordinations. The vegetation under oak canopies differs considerably from that in chaparral plots, as shown by relative frequencies of many species in oak versus chaparral plots (Appendix 1), and based on ordination scores for oak versus chaparral plots in a sample ordination including both plot types (Fig. 4). Characteristic species under oak canopies include the perennials, *Toxicodendron diversilobum*, *Baccharis pilularis*, *Galium nuttallii*, and *Marah fabaceus* (Appendix 1). The only annual that occurs with much greater frequency under oaks is *Claytonia perfoliata*. On the other hand, many annuals occur exclusively or preferentially in chaparral, for example, *Calyptridium monandrum*, *Camissonia strigulosa*, *Linaria canadensis* var. *texana*, and *Vulpia myuros* (Appendix 1).

The first DCA axis for the ordination based on annuals and biennials in oak understory plots is significantly related to the logarithm of time since burning ($r = 0.45$, $n = 21$, $p < 0.01$, Table 4). For perennial species under oaks, the first DCA axis is related to the logarithm of distance from the coast ($r = -0.51$, $n = 28$, $p < 0.05$), and plot age is not significantly associated with either DCA axis. We do not know whether distance from the coast or soil depth is the more important factor associated with perennial composition in oak understories.

The first DCA axis for the chaparral plot ordination based on woody perennial species is related to percent evergreen shrub cover ($r = -0.67$, $p < 0.001$), stand age ($r = -0.43$, $p < 0.01$), and soil pH ($r = 0.28$, $p < 0.05$) (Table 4). Vegetation changes are most rapid during the years immediately following fire, so that an improved linear relationship with DCA axis 1 is obtained by taking

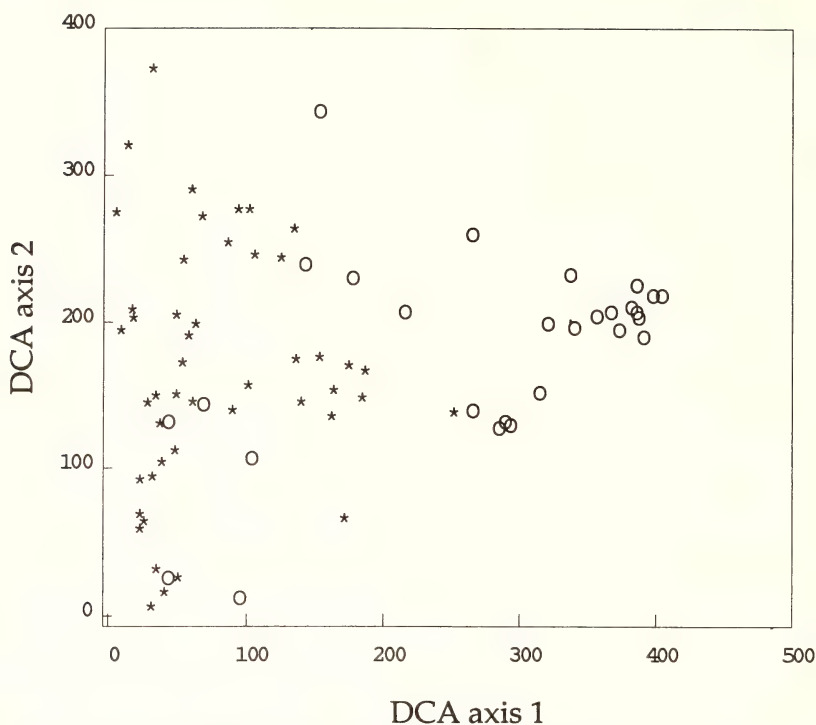


FIG. 4. DCA first versus second axis scores for plot ordination based on both chaparral (*) and oak plots (O).

the logarithm of stand age ($r = -0.53$). Two 25-year plots are severe outliers, one with unusually high cover of *Horkelia cuneata* and the other with low shrub diversity and dominance by *Ceanothus ramulosus* (although these plots had not been disturbed since last burning, they were mechanically cleared 40–50 years ago). Elimination of these outliers increases correlation of DCA axis 1 with the log of stand age to -0.69 . The second DCA axis for woody perennials is significantly related to soil depth ($r = 0.63$, $p < 0.001$), the logarithm of distance from the coast ($r = 0.61$, $p < 0.001$), and soil texture ($r = -0.39$, $p < 0.01$). The joint effects of these environmental variables are displayed by plotting their loadings on two canonical correlation axes, which have canonical correlations of 0.65 and 0.63 (Fig. 5). Plot age has the highest loading on axis 1, whereas plot depth has the highest loading on the second canonical axes. Distance and soil texture have moderate loadings; soil pH has the lowest score.

We have observed a strong association of soil depth and vegetation composition, with distance from the coast held constant, at some

TABLE 4. CORRELATIONS (r) OF PLOT SCORES ON THE FIRST AND SECOND DCA AXES WITH MEASURED ENVIRONMENTAL VARIABLES. Numbers in parentheses are sample size. Lower sample size for annual ordinations is due to the absence of annual species in some plots. Correlations significant at $p < 0.05$ indicated by asterisk. na—variable not measured at all plots.

Factor	Oak plots						Chaparral plots					
	Annuals (21)			Perennials (28)			Annuals (45)			Perennials (47)		
	DCA 1	DCA 2		DCA 1	DCA 2		DCA 1	DCA 2		DCA 1	DCA 2	
Years since burn	0.31	0.17		-0.22	-0.47*		0.43*	0.13		0.51*	0.03	
Log(yr since burn)	0.45*	0.13		-0.18	0.03		0.52*	0.17		-0.56*	0.10	
Soil depth	na	na		na	na		0.05	-0.55*		-0.05	0.63*	
Total shrub cover	na	na		na	na		0.67*	-0.02		-0.79*	-0.10	
Log(distance from coast)	0.05	-0.08		-0.51*	-0.01		0.12	-0.42*		0.09	0.61*	
Soil fine fraction	na	na		na	na		0.18	0.28		0.22	-0.39*	
Soil pH	na	na		na	na		0.07	0.12		0.28*	-0.16	

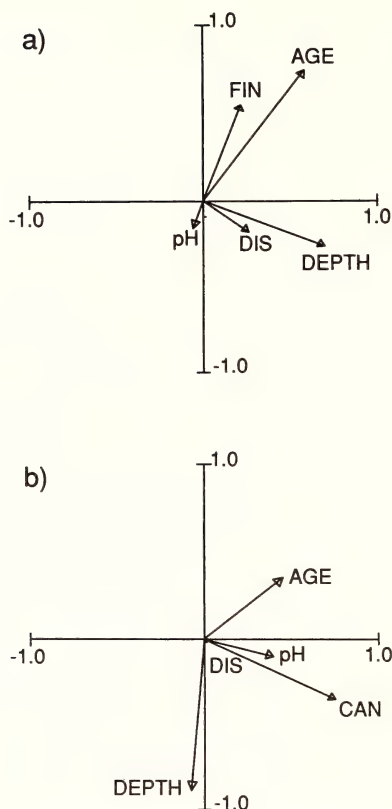


FIG. 5. Loadings of environmental variables on canonical correlation axes extracted jointly for environmental variables and chaparral plot scores in the first two DCA ordination axes. Environmental variables are standardized to $N(0, 1)$. The length of the arrow is proportional to the weighting of the variable in the canonical correlation function. a) Plot scores based on perennial species ordination. Canonical correlations are 0.65 and 0.63 for axes 1 and 2. DCA axis 1 loadings: $-0.48, -0.71$; DCA axis 2 loadings: $0.88, -0.69$. Environmental variables are log(years since fire) (AGE), log(distance from coast) (DIS), soil depth (DEP), percent fine fraction (FIN), and pH. b) Plot scores based on ordination of annual and biennial species. Canonical correlations are 0.77 and 0.58 for axes 1 and 2. DCA axis 1 loadings: $0.89, -0.16$; DCA axis 2 loadings: $0.44, 0.99$. CAN is total canopy cover by evergreen shrubs.

sites where soil grades from deep sand to shallow sand over a clay pan or bedrock. In older stands, we observed a gradient from *Adenostoma*-dominated to *Arctostaphylos*-dominated chaparral when moving from deep to shallow sand. On recently-burned sites, one can observe a decline in *Lotus scoparius* and an increase in *Helianthemum scoparium* on increasingly shallow soil.

We were unable to sample 10–25 year stands on very shallow soils, and also could not locate any 25–30-year-old stands. Never-

theless, the data indicate some strong patterns in the distribution of the dominant shrubs of Burton Mesa chaparral (Fig. 6). Canopy cover of *Ceanothus ramulosus* var. *fascicularis* peaked in stands between 10 and 25 years of age on deep sand. We encountered *C. impressus* only in plots that burned in the past 10 years on shallow soils. The highest cover values for *Arctostaphylos purissima* occurred in stands greater than 50 years of age on very shallow soil. *Arctostaphylos rudis* reached maximum cover in the oldest plots, but was not strongly associated with soil depth.

Chaparral plot ordinations based on annual species show many of the same patterns as those based on perennials, although the relationships are not as strong (Table 4). The first DCA axis is significantly related to stand age ($r = 0.43$, $p < 0.01$) and its logarithm ($r = 0.52$, $p < 0.01$), but is more clearly related to total cover of evergreen sclerophyllous shrubs ($r = -0.67$, $p < 0.001$). The second DCA axis based on annual species is significantly related to soil depth ($r = -0.55$, $p < 0.01$) and to the log of distance from the coast ($r = -0.42$, $p < 0.05$). Other soil variables are not strong predictors of vegetation composition. Evergreen shrub canopy cover and depth have the highest loadings in the canonical correlation axes, which have canonical correlations of 0.77 and 0.58 (Fig. 5). As with the canonical correlation analysis for perennial species, the relative importance of the different environmental variables is not especially sensitive to variable transformations.

Most annuals and biennials did not occur in very many plots and thus we cannot describe their distributions with much certainty. Also, micro-scale pattern in distribution of annual herbs, particularly in relation to shrub canopies and canopy gaps, makes it difficult to draw strong conclusions about their habitat associations based on their occurrence in 100 m² sample plots. Analysis of direct ordinations (not shown) indicates that some of the most frequent species are nearly ubiquitous, and their presence is not associated with plot age, soil depth or distance from the coast. These include *Camissonia micrantha*, *Chorizanthe diffusa* var. *nivea*, *Crassula erecta*, and *Vulpia octoflora*. Frequent species characteristic of younger, more open stands include *Hypochoeris glabra*, which occurs on all soils, and *Daucus pusillus* and *Pterostegia drymarioides*, which occur on shallow and deep soils, respectively. *Perezia microcephala* is a perennial herb species characteristic of older closed stands, and it occurs exclusively on deep, well-drained soils.

DISCUSSION

Fire regime. The present fire regime of the Burton Mesa is entirely anthropogenic. Modern land use is increasingly fragmenting the remaining chaparral into isolated patches, reducing potential fire size and probably increasing the average time between fires on a site.

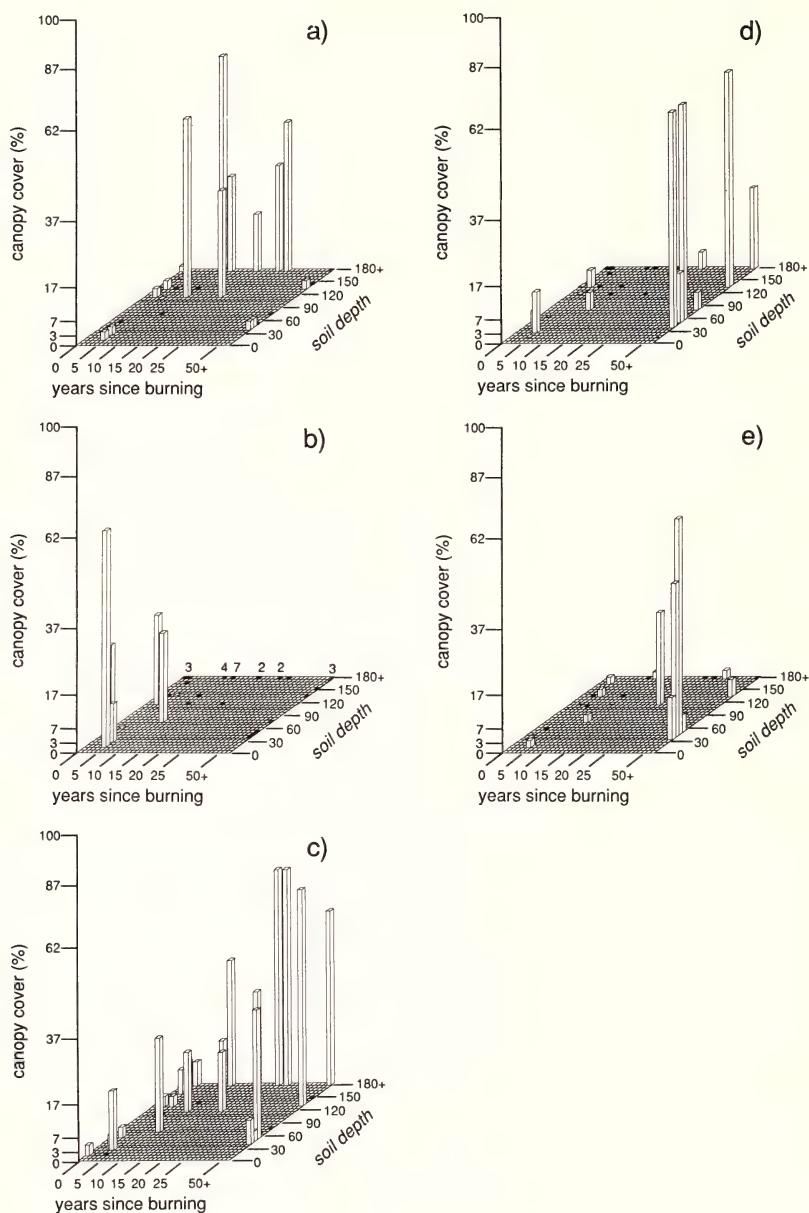


FIG. 6. Three-dimensional graphs of canopy cover versus stand age and soil depth for the 5 dominant canopy shrubs in Burton Mesa chaparral ($n = 47$): a) *Ceanothus ramulosus*, b) *C. impressus*, c) *Adenostoma fasciculatum*, d) *Arctostaphylos rudi*s, e) *A. purissima*. Cover values shown on the Z axis are midpoints of Braun-Blanquet cover classes. Shaded squares indicate species absence in a sample. Numbers along

With a long fire-recurrence interval coast live oak should increase on all but the driest sites in sandy coastal chaparral environments (Wells 1962, Griffin 1978). Our data support this interpretation for the central and eastern mesa. However, on very poorly drained soils and sites near the coast, oak cover is low even in the oldest plots sampled, implying that these areas persist as chaparral for long time periods.

Flora. Ferren et al. (1984) collected 342 taxa (252 native, 90 naturalized) from the range of upland and wetland habitats present in the eastern Burton Mesa. Our list of 152 species is not comprehensive but includes nearly all species occurring on unplowed and ungrazed uplands of the Burton Mesa. Numerous other species documented on the Burton Mesa, such as the common *Hordeum leporinum*, *Cnicus benedictus*, *Sisyrinchium bellum*, and *Juncus bufonius*, typically occur on previously disturbed sites, where the present vegetation is mostly introduced grassland or coastal scrub species.

The presence of 152 species within a total sample area of only 0.79 ha of level uplands is indicative of moderately high total richness of the Burton Mesa chaparral flora compared to other shrublands in Mediterranean climates (cf. Parsons and Moldenke 1975, Trabaud and Lepart 1980, Shmida 1981, Cowling 1983). Species richness is increased somewhat by addition of exotic species, but may be more related to the sandy oligotrophic substrate, which has been associated with exceptional richness in other coastal chaparral communities (Griffin 1978) and in similar areas of the Mediterranean region (Naveh and Whittaker 1979), Australia (George et al. 1979), and South Africa (Cowling 1983). High richness has also been attributed to the location of the Burton Mesa in a transitional region combining northern and southern California floras (Ferren et al. 1984).

Spatial and temporal variation in species richness for 100 m² plots makes it difficult to compare richness at this scale to other values reported in the literature. We note that average species richness on the Burton Mesa is close to the 29 spp./100 m² reported by Shmida and Whittaker (1981) for other California chaparral and is lower than in Mediterranean shrublands recognized for their high richness, such as South Africa renosteveld, a coastal shrubland on sandy soils [42.1 spp./100 m² (Cowling 1983)], and heathland on western Australian sand plains [46 spp./100 m² (George et al. 1979)].

Factors that have been analyzed to explain variation in species

←

the top margin of the figure base in figure b) are the number of replicates for that combination of stand age and soil depth >180 cm (bars are sample average for replicates).

richness in Mediterranean shrublands include climate, topography, soil texture, soil fertility, soil pH, time since burning, and grazing intensity. Our analysis is somewhat different in that samples are not recently cleared or grazed and share the same climate, topography, and geologic substrate. Under these conditions, time since burning is a significant but weak predictor of species richness in maritime chaparral. Radtke (1981) obtained a similar result for other chaparral types. Also, soil depth, texture, and pH are not significantly related to sample richness. However, total evergreen shrub cover is a strong predictor, accounting for 58% of total sample variance, perhaps due to differences in levels of allelopathic chemicals or herbivory (e.g., McPherson and Muller 1969, Halligan 1973, Christensen and Muller 1975, Davis and Mooney 1985).

Vegetation ordinations. Although we sampled a narrow range of topographic conditions on a single geologic substrate, there are important differences between samples in soil depth and distance from the coast, so that they cannot be arrayed as a simple chronosequence to reconstruct successional patterns of maritime chaparral after fire. For oak understory vegetation, we have identified one or two major axes of variation, time since burning and distance from the coast, and for chaparral plots we have identified two or three major axes of variation, stand age or shrub canopy cover, soil depth, and distance from the coast, that must be considered jointly in relation to vegetation composition. More replicates of the same age and environmental conditions are needed to document conclusively the vegetation dynamics in these different environments.

Chaparral composition has been associated with geologic substrate and soil properties such as fertility, texture, and chemistry (e.g., Wells 1962, O'Leary 1984, Beatty 1987). The edaphic variable most affecting chaparral composition on Burton Mesa is the depth of sand overlying bedrock or a subsoil pan. There are probably large differences in soil water regime between shallow and deep sands. We expect that shallow soils have low water holding capacity, perhaps remaining waterlogged during the winter and early spring, and then losing most of their water by late spring or early summer. The high water holding capacity of deep soils means that waterlogging does not occur, but that soil water remains available at depth in the profile later in the year (Nixon and Lawless 1960). Differences in soil fertility would also be expected due to differences in the extent of leaching. Soil fertility was not measured here, except indirectly by pH determination, and deserves more careful study (Christensen and Muller 1975, Parker 1977, O'Leary 1984).

Soil variation may partly explain the differentiation of the endemic congeners, *Ceanothus impressus* var. *impressus* versus *C. ramulosus* var. *fascicularis*, and *Arctostaphylos purissima* versus *A. rudis*. The

importance of edaphic variation in promoting narrow endemics was noted by Mason (1946). Wells (1969) has described rapid speciation by obligate seeding *Ceanothus* and *Arctostaphylos* on different substrates.

The association of many herb species with either chaparral or oak understories produces abrupt changes in herb layer composition at the edge of oak canopies, a pattern that is evident on all sites where oaks occur and at all stages of vegetation development after fire. We observed but did not measure additional within-stand pattern in the chaparral herb layer at the scale of canopy gaps and shrub understories (e.g., Shmida and Whittaker 1981). We are now analyzing local and microscale patterns in fire behavior, soil chemistry, and seed banks of chaparral and oak understories to help understand the origin of this microscale floristic pattern in maritime chaparral.

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APPENDIX 1. SPECIES LIST FROM SAMPLE PLOTS. **Vulpia megalura* and *V. myuros* were treated as a single entity by Lonard and Gould (1974). We treated them as separate taxa because they were readily distinguishable in the field, and there was some evidence of ecological differentiation between them.

Species	Family	Frequency	
		Shrub plots	Oak plots
Trees and shrubs			
<i>Adenostoma fasciculatum</i>	Rosaceae	87	39
<i>Arctostaphylos purissima</i> P. V. Wells	Ericaceae	47	14
<i>Arctostaphylos rudis</i>	Ericaceae	55	29
<i>Artemisia californica</i>	Asteraceae	11	4
<i>Baccharis pilularis</i> subsp. <i>consanguinea</i>	Asteraceae	38	54
<i>Ceanothus impressus</i> var. <i>impressus</i>	Rhamnaceae	21	11
<i>Ceanothus ramulosus</i> var. <i>fascicularis</i>	Rhamnaceae	72	36
<i>Cercocarpus betuloides</i>	Rosaceae	6	4
<i>Dendromecon rigida</i>	Papaveraceae	11	7
<i>Ericameria ericoides</i> (Less.) Jeps.			
subsp. <i>ericoides</i>	Asteraceae	51	29
<i>Leptodactylon californicum</i>	Polemoniaceae	19	7
<i>Mimulus aurantiacus</i> subsp. <i>lompocensis</i>	Scrophulariaceae	60	54
<i>Quercus agrifolia</i>	Fagaceae	13	100
<i>Rhamnus californica</i>	Rhamnaceae	21	29
<i>Rhamnus crocea</i>	Rhamnaceae	21	4
<i>Salvia mellifera</i>	Lamiaceae	57	14
<i>Sambucus mexicana</i>	Caprifoliaceae	0	18
<i>Toxicodendron diversilobum</i> (Torr. & A. Gray) Greene	Anacardiaceae	36	75
Subshrubs			
<i>Carpobrotus edulis</i> (L.) L. Bolus	Aizoaceae	15	11
<i>Corethrogyne filaginifolia</i>	Asteraceae	32	14
<i>Croton californicus</i> var. <i>californicus</i>	Euphorbiaceae	40	11
<i>Eriastrum densifolium</i> subsp. <i>elongatum</i>	Polemoniaceae	23	4
<i>Eriogonum parvifolium</i>	Polygonaceae	9	0
<i>Eriophyllum confertiflorum</i>	Asteraceae	55	50
<i>Erysimum suffrutescens</i> var. <i>lompocense</i>	Brassicaceae	9	7
<i>Galium andrewsii</i>	Rubiaceae	42	54
<i>Galium nuttallii</i>	Rubiaceae	62	79
<i>Helianthemum scoparium</i>	Cistaceae	66	21
<i>Horkelia cuneata</i>	Rosaceae	68	32
<i>Lotus scoparius</i> (and <i>L. junceus</i>)	Fabaceae	64	39
<i>Phacelia ramosissima</i> var. <i>suffrutescens</i>	Hydrophyllaceae	11	11
<i>Senecio douglasii</i>	Asteraceae	11	11
<i>Solanum douglasii</i>	Solanaceae	0	11
<i>Solanum umbelliferum</i>	Solanaceae	13	21
<i>Solanum xanti</i>	Solanaceae	2	11
Perennial herbs			
<i>Bloomeria crocea</i>	Amaryllidaceae	2	0
<i>Calochortus albus</i>	Liliaceae	2	0
<i>Calystegia macrostegia</i> subsp. <i>cyclostegia</i>	Convolvulaceae	2	4
<i>Carex globosa</i>	Cyperaceae	30	21
<i>Carex triquetra</i>	Cyperaceae	6	0

APPENDIX 1. CONTINUED.

Species	Family	Frequency	
		Shrub plots	Oak plots
<i>Chenopodium californicum</i>	Chenopodiaceae	0	7
<i>Chlorogalum pomeridianum</i>	Liliaceae	6	0
<i>Conicosia pugioniformis</i> (L.) N. E. Br.	Aizoaceae	2	4
<i>Cortaderia jubata</i> (Lem.) Stapf.	Poaceae	0	4
<i>Cuscuta californica</i>	Convolvulaceae	2	0
<i>Dichelostemma pulchellum</i> (Salisb.) Heller	Amoryllidaceae	23	0
<i>Dudleya lanceolata</i>	Crassulaceae	19	0
<i>Erigeron sanctarum</i>	Asteraceae	34	28
<i>Fritillaria biflora</i>	Liliaceae	4	0
<i>Gnaphalium beneolens</i>	Asteraceae	17	4
<i>Gnaphalium bicolor</i>	Asteraceae	11	0
<i>Juncus textilis</i>	Juncaceae	0	4
<i>Marah fabaceus</i> var. <i>agrestis</i>	Cucurbitaceae	23	71
<i>Melica imperfecta</i>	Poaceae	32	29
<i>Paeonia californica</i>	Paoniaceae	19	18
<i>Pedicularis densiflora</i>	Scrophulariaceae	4	0
<i>Penstemon centranthifolius</i>	Scrophulariaceae	4	0
<i>Perezia microcephala</i>	Asteraceae	19	11
<i>Pityrogramma triangularis</i>	Pteridaceae	2	0
<i>Pteridium aquilinum</i> var. <i>pubescens</i>	Pteridaceae	13	14
<i>Rumex angiocarpus</i>	Polygonaceae	2	0
<i>Sanicula bipinnatifida</i>	Apiaceae	2	4
<i>Sanicula crassicaulis</i>	Apiaceae	0	4
<i>Silene laciniata</i> subsp. <i>major</i>	Caryophyllaceae	17	14
<i>Stipa cernua</i>	Poaceae	2	0
<i>Zigadenus fremontii</i>	Liliaceae	15	29
Annual and biennial herbs			
<i>Amsinckia spectabilis</i> var. <i>microcarpa</i>	Boraginaceae	2	4
<i>Anagallis arvensis</i>	Primulaceae	28	18
<i>Apiastrum angustifolium</i>	Apiaceae	17	21
<i>Arenaria douglasii</i>	Caryophyllaceae	2	0
<i>Avena barbata</i>	Poaceae	4	7
<i>Bromus diandrus</i>	Poaceae	6	11
<i>Bromus mollis</i>	Poaceae	9	0
<i>Bromus rubens</i>	Poaceae	43	32
<i>Calandrinia breweri</i>	Portulacaceae	2	4
<i>Calyptidium monandrum</i>	Portulacaceae	15	4
<i>Camissonia micrantha</i>	Onagraceae	68	32
<i>Camissonia strigulosa</i>	Onagraceae	19	4
<i>Centaurea melitensis</i>	Asteraceae	0	4
<i>Centaurium davyi</i>	Gentianaceae	2	0
<i>Chorizanthe californica</i>	Polygonaceae	15	4
<i>Chorizanthe coriacea</i>	Polygonaceae	2	4
<i>Chorizanthe diffusa</i> Benth. var. <i>nivea</i> (Curran) Hoover	Polygonaceae	74	25
<i>Cirsium californicum</i>	Asteraceae	2	4
<i>Cirsium occidentale</i> var. <i>occidentale</i>	Asteraceae	13	14
<i>Claytonia perfoliata</i> (Donn) Howell	Portulacaceae	15	54
<i>Conium maculatum</i>	Apiaceae	0	4

APPENDIX 1. CONTINUED.

Species	Family	Frequency	
		Shrub plots	Oak plots
<i>Conyza canadensis</i>	Asteraceae	17	25
<i>Cordylanthus rigidus</i> (Benth.) Jeps. subsp. <i>littoralis</i> Chuang & Heckard	Scrophulariaceae	4	0
<i>Crassula erecta</i> (H. & A.) Berger	Crassulaceae	70	21
<i>Cryptantha clevelandii</i>	Boraginaceae	53	43
<i>Daucus pusillus</i>	Apiaceae	32	36
<i>Descurainia pinnata</i> ssp. <i>menziesii</i>	Brassicaceae	11	21
<i>Eriophyllum multicaule</i>	Asteraceae	4	0
<i>Erodium botrys</i>	Geraniaceae	4	0
<i>Erodium cicutarium</i>	Geraniaceae	21	11
<i>Filago californica</i>	Asteraceae	70	18
<i>Filago gallica</i>	Asteraceae	40	18
<i>Galium aparine</i>	Rubiaceae	2	7
<i>Gastridium ventricosum</i>	Poaceae	0	4
<i>Gilia austrooccidentalis</i>	Polemoniaceae	30	7
<i>Gnaphalium californicum</i>	Asteraceae	6	11
<i>Gnaphalium luteo-album</i>	Asteraceae	2	0
<i>Gnaphalium purpureum</i>	Asteraceae	13	14
<i>Gnaphalium ramosissimum</i>	Asteraceae	17	25
<i>Hesperocnide tenella</i>	Urticaceae	2	4
<i>Heterotheca grandiflora</i>	Asteraceae	6	0
<i>Hypochoeris glabra</i>	Asteraceae	51	25
<i>Koeleria phleoides</i>	Poaceae	4	0
<i>Layia glandulosa</i>	Asteraceae	9	7
<i>Layia paniculata</i>	Asteraceae	2	0
<i>Linaria canadensis</i> var. <i>texana</i>	Scrophulariaceae	26	4
<i>Loeflingia squarrosa</i>	Caryophyllaceae	9	0
<i>Lotus hamatus</i>	Fabaceae	4	0
<i>Lotus strigosus</i>	Fabaceae	32	18
<i>Lupinus bicolor</i>	Fabaceae	2	4
<i>Lupinus truncatus</i>	Fabaceae	6	0
<i>Madia exigua</i>	Asteraceae	2	4
<i>Malacothrix californica</i>	Asteraceae	9	7
<i>Malacothrix clevelandii</i>	Asteraceae	4	4
<i>Melilotus indica</i>	Fabaceae	0	7
<i>Microseris heterocarpa</i>	Asteraceae	2	4
<i>Microseris linearifolia</i>	Asteraceae	9	4
<i>Mimulus subsecundus</i>	Scrophulariaceae	2	0
<i>Navarretia atractylodes</i>	Polemoniaceae	51	18
<i>Orthocarpus purpurascens</i>	Scrophulariaceae	2	0
<i>Pectocarya penicillata</i>	Boraginaceae	2	0
<i>Phacelia douglasii</i>	Hydrophyllaceae	2	4
<i>Plagiobothrys</i> sp.	Boraginaceae	2	0
<i>Plantago erecta</i>	Plantaginaceae	2	0
<i>Polycarpon depressum</i>	Caryophyllaceae	28	4
<i>Polypogon monspeliensis</i>	Poaceae	2	0
<i>Pterostegia drymarioides</i>	Polygonaceae	36	29
<i>Rafinesquia californica</i>	Asteraceae	15	21
<i>Salvia columbariae</i>	Lamiaceae	9	0

APPENDIX 1. CONTINUED.

Species	Family	Frequency	
		Shrub plots	Oak plots
<i>Schismus barbatus</i>	Poaceae	2	0
<i>Scrophularia</i> sp.	Scrophulariaceae	2	0
<i>Senecio californicus</i>	Asteraceae	9	11
<i>Senecio vulgaris</i>	Asteraceae	2	7
<i>Silene gallica</i>	Caryophyllaceae	2	0
<i>Sonchus asper</i>	Asteraceae	13	18
<i>Sonchus oleraceus</i>	Asteraceae	2	11
<i>Stellaria media</i>	Caryophyllaceae	0	7
<i>Stylocline gnaphalioides</i>	Asteraceae	11	4
<i>Thelypodium lasiophyllum</i>	Brassicaceae	0	4
<i>Trifolium microcephalum</i>	Fabaceae	2	0
<i>Trifolium</i> sp.	Fabaceae	0	4
<i>Vulpia bromoides</i> (L.) S. F. Gray	Poaceae	15	4
* <i>Vulpia megalura</i> Nutt.	Poaceae	23	18
<i>Vulpia microstachys</i> (Nutt.) Benth.			
var. <i>ciliata</i> (Beal) Lonard & Gould	Poaceae	0	4
* <i>Vulpia myuros</i> (L.) C. C. Gmelin	Poaceae	15	0
<i>Vulpia octoflora</i> (Walt.) Rydb.	Poaceae	66	39

ANNOUNCEMENT

SIXTH WILDLAND SHRUB SYMPOSIUM

The Shrub Research Consortium is sponsoring the Sixth Wildland Shrub Symposium, 5-7 April 1989, at the Holiday Inn, Las Vegas, NV. The symposium will address topics in wildland shrub biology and management including cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management. A field trip is planned to the Nevada Test Site of the U.S. Department of Energy. Both contributed and invited papers will be presented. Contributed presentations will be 20 minutes. The proceedings will be published by the USDA Forest Service, Intermountain Research Station.

If you would like to present a paper, send a title and abstract by 15 December 1988, to Dr. E. M. Romney, Laboratory of Biomedical and Environmental Sciences, University of California, Los Angeles, 900 Veteran Avenue, Los Angeles, CA 90024. To receive preregistration materials and information please contact Keith McNeil, Division of Continuing Education, University of Nevada, Las Vegas, 4505 University Parkway, Las Vegas, NV 89154; (702) 739-3707.

INVASION OF *CARPOBROTUS EDULIS* AND
SALIX LASIOLEPIS AFTER FIRE IN A
COASTAL CHAPARRAL SITE IN
SANTA BARBARA COUNTY,
CALIFORNIA

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ABSTRACT

Observations in permanent plots after a 1982 controlled fire in chaparral vegetation in coastal Santa Barbara County, California demonstrate that *Carpobrotus edulis*, the common introduced ice plant, increased substantially along with other native plants capable of invading disturbed sites such as *Salix lasiolepis*. Although fire is a natural disturbance, it can favor the spread of invasive exotics when a seed source is available. Controlled burning programs must consider the possibility and risks of invasion by exotics.

The importance of human disturbances such as grazing, agriculture, and road construction in promoting the invasion of exotics is well known (Elton 1958). It is less clear if natural disturbance factors such as fire hinder or assist invasion (Johnstone 1986). A well-accepted explanation for weed invasion is that human disturbance creates a new environment in which the native plants are at a disadvantage with respect to invaders. Thus, the argument can be made that fire in a landscape where it has a long history should not give an advantage to exotics. On the contrary, the native plants, which are presumably fitted to the special local characteristics of the fires, might be favored. This theoretical reasoning is given practical support by burning experiments that have shown a decrease in exotics (e.g., Hillyard 1985). It is the purpose of this paper to demonstrate that burning by no means inevitably favors natives and may, in some instances, promote the spread of exotics.

The exotic studied here, *Carpobrotus edulis* (L.) Bolus ("ice plant"), has been widely planted in California and is now viewed as a weed (McClintock 1985) that should be eradicated in sensitive natural habitats (e.g., Libby 1979). It is particularly aggressive in sandy coastal sites (Griffin 1978), where it can become the dominant plant over large areas. Populations of an exotic succulent plant such as *C. edulis* might be expected to decrease with burning, and fire might be expected to serve as a means of controlling this species. Our results show, on the contrary, that fire can favor its expansion.

STUDY AREA

The study was conducted on Burton Mesa in Santa Barbara County, California (34°42'30"N, 120°43'W) about 2.6 km from the ocean to the west of the railroad tracks near the intersection of 35th Street and California Boulevard on Vandenberg Air Force Base. The soil type at the site is mapped as Tangair with inclusions of the poorly-drained Narlon series (Shipman 1972). Both soils have coarse sandy loam textures, are derived from marine deposits, and are low in fertility.

The vegetation at the site is a distinctive central-coast phase of chaparral. It is characterized by low, sometimes salt-spray trimmed canopies of evergreen species with an admixture of drought-deciduous coastal sage scrub elements. The site also includes other species of limited or disjunct distribution, such as *Arctostaphylos rudis* and *Eriodictyon capitatum*.

METHODS

The data reported here were collected in conjunction with an experimental burn of approximately 40 ha conducted in the summer of 1982 to determine the effect of prescribed fire on *E. capitatum* (Jacks, Zedler, and Scheidlinger unpubl. report). Before the fire, a sample area of approximately 0.6 ha, delimited by clearing along a paved road, a railroad track, and an old unpaved track, was selected and divided into two plots of about 2500 and 3600 sq m, the larger of which was left unburned. A 100 m transect, crossing both the burned and unburned vegetation, was established in June 1982 before the fire and was sampled for crown cover. In addition to marking individual *E. capitatum* to follow in survivorship studies, we established four 3 × 3 m plots in the burn area centered on *E. capitatum* clumps. These plots were therefore not random with respect to *E. capitatum* but were not selected with reference to *C. edulis*. The cover of all shrub species within these plots was recorded and the locations of all *E. capitatum* were mapped before the fire. After the fire, seedlings and sprouts were mapped.

We estimated seed production of *C. edulis* in 1985 by counting the number of fruits in 40 regularly spaced meter-square quadrats, collecting 3 fruits from each quadrat in which they were present, and counting the seeds in a randomly selected sub-sample of 12 fruits.

RESULTS

In 1982, before the fire, *C. edulis* was present along the road and the railway that bordered the site. No *C. edulis* plants were recorded within the experimental area, however, which had a nearly complete

TABLE 1. PRE- AND POST-BURN COVER OF SHRUBS, SUB-SHRUBS, AND *Carpobrotus edulis* ON A CHAPARRAL SITE ON VANDENBERG AIR FORCE BASE, SANTA BARBARA COUNTY, CALIFORNIA. Transect lengths were 60 m for 1982 and 100 m for 1985. Live cover values include overlap. Bare ground is area not covered by live or dead plant canopies. Nomenclature after Smith (1976).

Species	Pre-burn 1982 cover (%)		Post-burn 1985 cover (%)	
	Live	Dead	Live	Dead
<i>Adenostoma fasciculatum</i>	45.3	1.2	4.3	0.0
<i>Arctostaphylos purissima</i>	39.3	0.3	1.1	0.0
<i>Arctostaphylos rudis</i>	15.9	1.7	1.0	0.0
<i>Carex</i> sp.	0.0	0.0	0.3	0.0
<i>Carpobrotus edulis</i>	0.0	0.0	26.2	0.3
<i>Ceanothus impressus</i>	0.0	0.0	0.1	0.0
<i>Ceanothus ramulosus</i>	1.2	2.6	0.5	0.0
<i>Eriodictyon capitatum</i>	3.2	1.2	1.7	0.0
<i>Haplopappus ericoides</i>	1.0	0.1	0.0	0.0
<i>Helianthemum scoparium</i>	0.0	0.0	30.4	1.9
<i>Lotus scoparius</i>	0.0	0.0	3.0	0.9
<i>Salvia mellifera</i>	3.9	0.4	3.6	0.0
Bare ground	1.8	—	33.1	—

cover of living or dead shrub canopies of primarily evergreen species (Table 1). Because of this dense cover, we cannot assert that *C. edulis* was not present somewhere in the experimental area, but there is no doubt that its total density was negligible. In contrast, in 1985, three years after the fire, the cover of *C. edulis* was 26%, making it the second-most prevalent post-fire perennial plant (Table 1).

Observations in the permanent plots confirm that seedling establishment is responsible for the increase in *C. edulis*. These plots were resampled in 1983, and the location of *C. edulis* and shrub seedlings was recorded (Table 2). Seedlings of *C. edulis* were recorded at an average density of over 7000/ha. A 1985 resample relocated 70% of these, indicating a high survivorship. Three new plants of *C. edulis* were found in 1985 that may have been established in the second season of recovery but more probably were missed in the initial survey.

Although *C. edulis* has been reported to reproduce only vegetatively (McClintock 1985), the observed seedling establishment obviously contradicts this. We collected fruits and found an average of 5.3 (s.d. = 12.1, $n = 40$) fruits/m² and an average of 1004 seeds/fruit (s.d. = 431, $n = 12$). This indicates a 1985 seed production of over 5.3 million seeds/ha. This figure can be expected to vary from year to year and place to place, but the numbers serve to show that *C. edulis* can have prodigious seed production.

Coastal sage scrub communities are particularly vulnerable to changes in species composition (i.e., invasion) when, as in this case,

TABLE 2. ABUNDANCE OF SEEDLINGS IN PERMANENT QUADRATS NOTED IN JULY 1983 AFTER THE SUMMER 1982 PRESCRIBED BURN. Values are based on averages of four 3 × 3 m plots. s.e. represents the standard error of the mean for the sample of four plots.

Species	Number/ha	s.e.
<i>Arctostaphylos rudis</i>	2230	4450
<i>A. purissima</i>	41,075	18,000
<i>Adenostoma fasciculatum</i>	1650	1650
<i>Salvia mellifera</i>	6930	2700
<i>Ceanothus ramulosus</i>	825	830
<i>C. impressus</i>	1375	1380
<i>Salix lasiolepis</i>	6400	715
<i>Baccharis pilularis</i>	4425	1211
<i>Lotus scoparius</i>	3600	1895
<i>Carpobrotus edulis</i>	7780	2100
<i>Solanum xanthii</i>	4700	1470

the vegetation is composed mainly of species with no ability (e.g., *Ceanothus ramulosus*, *Arctostaphylos purissima*) or only a weak ability (e.g., *Salvia mellifera*) to resprout after fire (Westman and O'Leary 1986). The establishment of several other species is evidence of this susceptibility of burned coastal sage chaparral to invasion. The presence of seedlings of *Salix lasiolepis* in the burned area was very unexpected (Table 2). No mature individuals of this species were observed anywhere within a kilometer of the site before or after the fire. The identity of the species was confirmed, however, by comparison with seedlings found along the Santa Ynez River, where the species is very abundant. We assume that the seeds were blown onto the site from these large stands along the Santa Ynez River which lies about 2 km to the south.

It is not surprising that willow seeds dispersed to the site and germinated there. What is more remarkable is that they established and survived to early July 1983, and that a few were still present and alive in the area the following summer. The mortality in the permanent plots was, however, complete by the second summer. The initial survival of the willows probably was aided by the fact that the 1982–83 hydrologic year for the area was one of above-normal precipitation (81.9 cm; mean rainfall is 35.2 cm), and it may have been enhanced by the presence of a heavy clay layer overlying shale bedrock that underlies the sandy surface soil at a depth of a meter or more. The clay layer may have allowed high moisture conditions to persist in the first summer. This wet year was followed by 2 years of below-average precipitation (1983–84, 21.6 cm; 1984–85, 26.5 cm) which, in part, may explain the lack of willow establishment.

Other exotic species besides *C. edulis* were observed in the burn area. A number of *Eucalyptus* sp. seedlings, whose seeds evidently

dispersed from a nearby windbreak, were present as were the exotics *Cortaderia* sp. and *Herrea elongata*.

Two readily dispersed native species, *Baccharis pilularis* (wind-dispersed) and *Solanum xantii* (animal-dispersed) were common as seedlings in the post-fire vegetation (Table 2) even though they were minor elements as mature shrubs before the fire. These species are frequent in chaparral and coastal sage scrub, and it is questionable whether their presence constitutes "invasion".

DISCUSSION

The substantial cover of *C. edulis* after the 1982 fire is evidence that the invasion of exotic species into native vegetation can be advanced, rather than retarded by burning. The success of *C. edulis* as an invader is probably explained by its evolution with fire. Observations on *Carpobrotus* spp. in South Africa and Australia, where they are native, show that they often establish from seed after fire. Eugene Moll (pers. comm. 1985) of the University of Cape Town has noted post-fire seedling establishment of *C. dinidiata* in the sand plain and mesic mountain fynbos communities in South Africa, although he notes that the species is most abundant in communities that are seldom burned. Judith Brown of the Western Australian Wildlife Research Centre (pers. comm. 1985) reports that *C. edulis*, also introduced into W. Australia, establishes by seed after hot fires in coastal locations near Perth, although in her opinion it is "not an aggressive colonizer". Native species of *Carpobrotus*, however, can invade woodlands after fire. In one case on Middle Island off the coast of W. Australia a thick carpet of *Carpobrotus* developed from seedlings after fire in a *Eucalyptus angulosa*-*E. platypus* forest unburned for 170 years. This evidence suggests that invasion of *C. edulis* into burned chaparral at Vandenberg AFB may not be as anomalous as it appears.

Although fire provided the "temporary invasion window" (Johnstone 1986) there must also be propagules to exploit it. We do not know how and when the seeds of *C. edulis* dispersed to the site. Fruits of *C. edulis* are eaten by small mammals (W. Ferren pers. comm.) and the seeds are small and hard-coated. We suspect that most of the seeds were deposited at the site in small mammal feces. Therefore, the majority of the seeds probably were in the soil for some time before the fire.

It is known that fire can be used to decrease exotics in coastal settings. W. James Berry of the State Department of Parks and Recreation (pers. comm. 1985) reports several successes in controlling introduced species—*Avena* at Pt. Mugu and Malibu, *Bromus diandrus* at Montaña de Oro, and *Brassica* at Pt. Lobos. Timing was a key element in these efforts. The burns were conducted when they

would kill most of the seed crop of the exotics without seriously harming the desirable species, mostly perennial natives.

Our observations make it clear that these successes must not be taken as an indication that fire will inevitably act to the favor of natives over exotics. A case in point comes from South Africa where the native vegetation is well adapted to survive fire, but invasion of exotics, including pines from the Northern Hemisphere and *Hakea* from Australia, has become a serious problem. Fire can be used to reduce the abundance of some of these invaders, but others (e.g., *Acacia*) cannot be eliminated with burning (Kruger and Bigalke 1984).

It is also apparent that edge effects were important in the situation we describe. Human disturbance along the margins of the experimental plot allowed the populations of *C. edulis* to establish and maintain themselves. Fire provided the opportunity for the seedlings to establish. These results underline the importance of minimizing edge to area ratios in retarding the expansion of exotics. They also suggest that longer fire rotations should be favored over shorter rotations when undesirable exotics that require open conditions for establishment are present.

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THE VEGETATION AND ALPINE VASCULAR FLORA OF THE SAWATCH RANGE, COLORADO

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ABSTRACT

The Sawatch Range, located in central Colorado, is part of the Southern Rocky Mountains. Extending over 130 km in a north-south direction and 65 km in an east-west direction, the range is the highest and one of the most extensive in the state. No previous floristic work has been done on its tundra. Sixteen study areas distributed throughout the entire range were analyzed over four field seasons. A vascular flora of 289 taxa in 118 genera and 35 families is reported. Two taxa are recent new records for the state. Eight taxa are Colorado endemics. Sixteen taxa are limited to calcareous substrates within the range. The phytogeographic distribution of the flora is primarily alpine (38.1%) and western North American (31.5%). According to Sorensen's Index of Similarity, the floristic inventory of the Sawatch Range shows an overall consistency among the tundra vascular floras of the Mosquito and West Elk Ranges, Indian Peaks area of the Front Range, and the San Juan Mountains.

The Sawatch Range of central Colorado (Fig. 1), a segment of the Southern Rocky Mountains, extends over 130 km in a north-south direction between the valleys of the Eagle River on the north and Tomichi Creek on the south. The Arkansas River valley forms the eastern boundary of the 65 km wide range (Chronic and Chronic 1972); the Gunnison Basin, Taylor Park, and the Elk Mountains form the boundary on the west. Much of the 8450 sq. km area included within the Sawatch Range lies above timberline. The range lies between 38°30' and 39°40'N latitude and 106°10' and 106°50'W longitude. The Continental Divide follows the range for more than two-thirds of its length (Stark 1934). The Sawatch Range is the highest range in the state. It contains four of the state's five highest peaks and 15 of the state's 54 peaks that are over 4270 m.

The topography of the range is rugged and variable with a maximum relief of over 2135 m from the summits of the highest peaks to the floor of the Arkansas River valley (Stark and Barnes 1935). Extensive Pleistocene alpine and valley glaciers carved numerous cirques and scoured broad glacial troughs on both sides of the range. However, the rounded summit of Mt. Elbert, Colorado's highest mountain at 4401 m, extended beyond the upper limit of glaciation (Stark and Barnes 1935). Glacial erosional forms in the present alpine landscape include cirques, tarns, basins, hanging tributary valleys, and broad U-shaped valleys. Depositional landforms of gla-

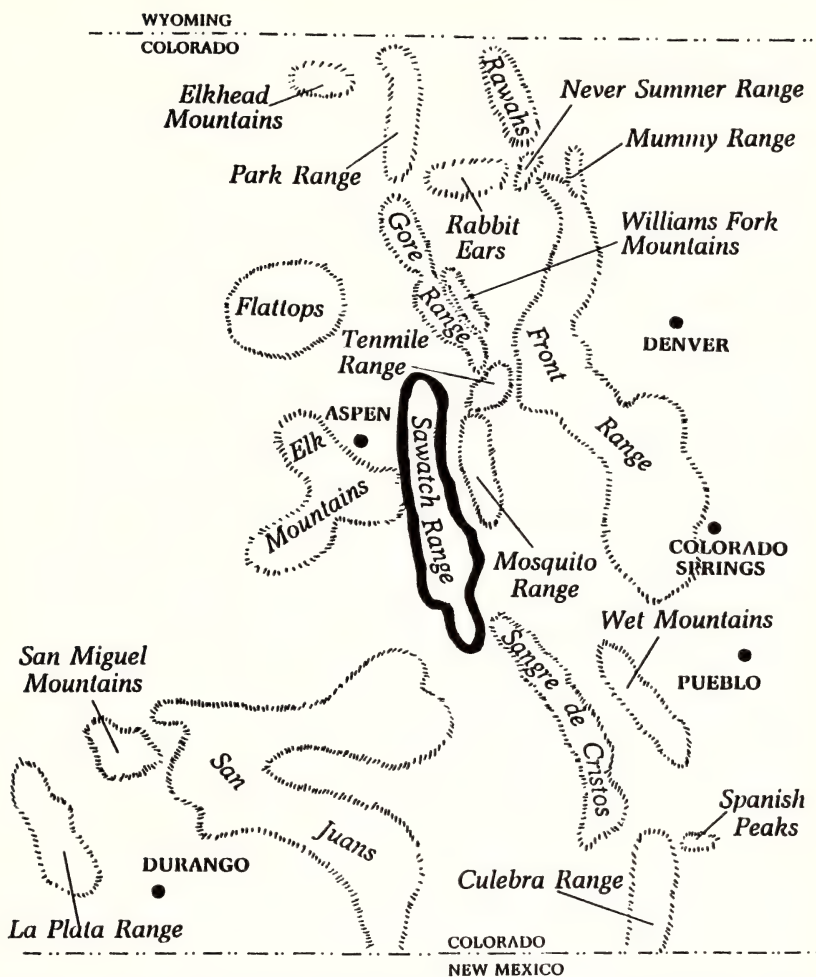


FIG. 1. Map showing the location of the Sawatch Range in the Southern Rocky Mountains of Colorado. (Courtesy of U.S.G.S.)

cial origin consist of both terminal and lateral moraines, some of which reach heights up to 305 m (Westgate 1905).

The Sawatch Range is composed primarily of coarse schists and gneisses intruded by pre-Cambrian granites, and of metamorphosed limestone and quartzite. Paleozoic sediments, including limestones, sandstones, and shales, dip away from the crystalline core on both sides of the range. Tertiary igneous intrusive rocks include stocks of quartz monzonite porphyry and various porphyritic dikes and sills. Extrusive rocks are highly localized: rhyolite occurs in the Independence Pass area in the north, and volcanic breccia occurs in

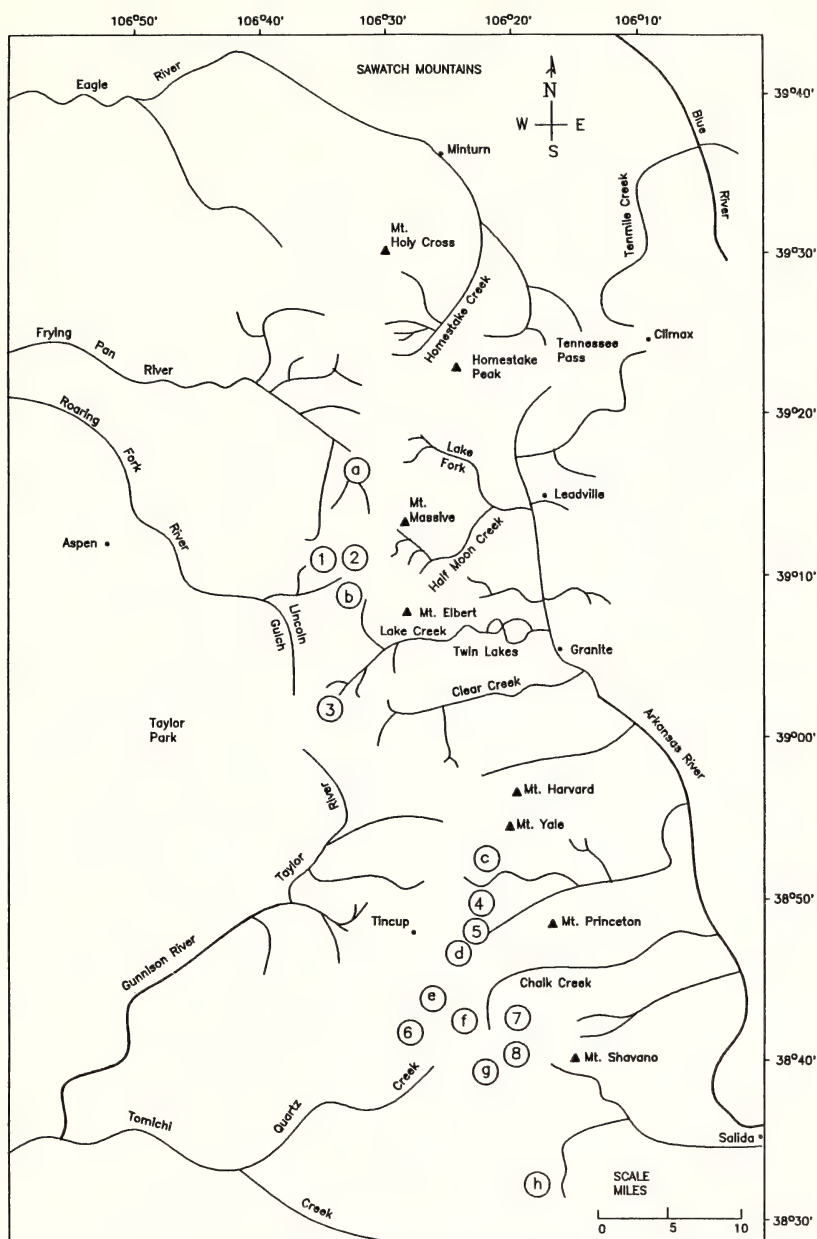
the southern part of the range near Tomichi Creek (Stark and Barnes 1932, 1935, Stark 1934, Brock and Barker 1972, Tweto 1974, Van Loenen 1985).

Climatic data from the Sawatch Range are non-existent. However, one can extrapolate data from a climograph for timberline elevation of 3446 m at Climax, Colorado, located 16 km east of the Sawatch Range (Arno and Hammerly 1984). Mean average temperature is -1.0°C and mean average precipitation is 149 cm. The climate of the Sawatch Range is typical of high mountainous areas in Colorado. Summer thunderstorms, often accompanied by hail, occur almost daily. Snowfall begins in September with major accumulations by mid-October and continuing until late May or early June. Daytime temperatures in the summer are temperate but frost may occur any night (Dings and Robinson 1957).

Our investigation is the first floristic study of the alpine tundra of the Sawatch Range. An ecological study by Loder (1964) was limited to an area on Cottonwood Pass. The primary objective of this study was to inventory the vascular flora of the alpine tundra of the Sawatch Range, thus filling in a noticeable gap in the tundra flora of the central mountainous area of Colorado. The importance of this range in expanding our knowledge of the Colorado tundra is amplified by the pivotal position the range occupies between the drier north-south oriented ranges to the east and the more moist east-west oriented ranges to the west. This study is part of our comprehensive floristic inventory of all of the tundra areas of the major mountain ranges in Colorado.

METHODS

This study was conducted over four field seasons: 1982, 1984, 1985, and 1986. The entire 1986 season, from 10 June through 10 October, was devoted to intensive field work in the range. The authors follow the definition of alpine tundra as the area above the subalpine forest on all peaks, ridges, and in basins that rise above the general level of tree-limit at an elevation of about 3477 m in Colorado; however, scattered *krummholz* conifers may extend as isolated patches or cushions into the alpine tundra zone (Marr 1961, Zwinger and Willard 1972, Arno and Hammerly 1984). In the Sawatch Range tree-limit is found to vary from 3629 m in the lower portions of the basins to 3782 m on the highest slopes. Sixteen alpine areas including eight passes and eight cirque basins distributed throughout the length of the Sawatch Range were selected for study (Fig. 2). The passes are basically saddles flanked by convex slopes and are relatively homogeneous in habitats and associated community types. Patterned ground forms, including sorted stripes, polygons, and frost boils, are common. Cirque basins which include basin



Drawn by: Dale Boody & Associates, Canon City, Colorado 3-30-87

FIG. 2. Map of the Sawatch Range, Colorado, showing study areas. Letters indicate passes; numbers indicate basins.

TABLE 1. LOCATION, ORIENTATION, AND ELEVATION OF STUDY AREAS IN THE SAWATCH RANGE, COLORADO.

Map reference	Location—pass	Orientation	Elevation (m)
a	Hagerman	e./w.	3637
b	Independence	e./w.	3689
c	Cottonwood	nnw./sse.	3698
d	Tincup	wnw./ese.	3707
e	Cumberland	n./s.	3663
f	Altman	nne./ssw.	3642
g	Hancock	n./s.	3691
h	Monarch	n./s.	3629

Map reference	Location—basin	Orientation	Elevational range (m)
1	Linkins Lake	se.	3660–3721
2	Mt. Champion	e.	3614–3798
3	Peekaboo	ne.	3538–3752
4	Mineral	se.	3733–3904
5	Emma Burr	e.	3736–3813
6	Fairview Peak	ne.	3599–3691
7	Billings Lake	se.	3569–3736
8	Island Lake	n.	3630–3691

floors, adjacent slopes, headwalls, and ridge tops, on the other hand, contain a greater diversity of habitats and community types. Cirque basins in the Sawatch Range tend to have a broader and more shallow morphology resulting in a more gradual drainage gradient than cirque basins in other mountain ranges of the state (Hartman and Rottman 1985a,b, 1987). Table 1 gives the orientation and elevation of the passes and the orientation and elevational ranges of the basin study areas.

A total of 825 communities representative of nine community types found in the Sawatch Range were inventoried in the study. The community types include dry, moist, and wet meadows, shrub tundra, krummholz, fellfield, rock-predominating (ledges, rock crevices, and talus), rivulet, and snowbank. Care was taken to ensure that the number of communities inventoried was proportionate to the predominance of the community type in each study area.

Identification of questionable taxa were verified by R. D. Dorn, R. L. Hartman, R. A. Price, R. C. Rollins, and W. A. Weber. A complete voucher set for all taxa inventoried in the Sawatch Range is deposited in the herbarium of the University of Colorado—Denver, where the authors are associated. In addition duplicates of most specimens are deposited in COLO. Nomenclature, for the most part, follows Nelson and Hartman (1987). The Colorado endemics, alternative names for taxa in the checklist, and 22 taxa not found in

Nelson and Hartman (1987) and indicated by an asterisk after the authority follow Weber (1987) and Wittmann et al. (1988).

VEGETATION

Meadow communities. The dry meadow community type is most common in the tundra of the Sawatch Range, unlike the moist meadow type which predominates in the ranges to the west and southwest in Colorado (Langenheim 1962, Webber et al. 1976, Rottman and Hartman 1985, Hartman and Rottman 1987). Dry meadows predominate on passes, on convex mountain slopes, and on the upper slopes of cirque basins. The predominance of dry meadows in the Sawatch correlates with the Mosquito Range adjacent to the Arkansas River valley on the east (Hartman and Rottman 1985a). We anticipated finding different dominants in the dry meadows on passes than in those in basins; however, *Kobresia bellardii*, *Dryas octopetala* var. *hookeriana*, *Geum rossii* var. *turbinatum*, *Carex elynoides*, and *Salix reticulata* subsp. *nivalis* occur in both. The only slight difference found is that *Kobresia bellardii*, the most frequent dominant on the passes, is replaced by *Dryas octopetala* var. *hookeriana* in the basins. The listed dominants appear to vary with local microenvironments which are not exposure correlated. Among the graminoid taxa, grasses exceed sedges only in dry meadows. Closed turf communities dominated by *Kobresia bellardii* or *Carex elynoides* have a low species richness.

Moist meadow dominants occur in three size classes: an erect tall form such as *Deschampsia caespitosa*, a short caespitose form represented by *Carex nigricans*, and a prostrate semi-shrub form typical of *Sibbaldia procumbens* and *Salix reticulata* subsp. *nivalis*. Moist meadows on the passes are restricted to swales where *Deschampsia caespitosa* is dominant and on the concave bases of pass slopes where either *Sibbaldia procumbens* or *Salix reticulata* subsp. *nivalis* predominate. In the basins this community type occupies the mid- to lower slopes and borders the basin floor where it may interdigitate with shrub tundra or wet meadow. *Deschampsia*-dominated moist meadow communities in the basins are associated with a wide variety of tall forb taxa including *Erigeron peregrinus* subsp. *callianthemus*, *Potentilla diversifolia*, and *Senecio crassulus*. *Carex nigricans* and *Sibbaldia procumbens* are often co-dominant where basin slope and floor interface.

Wet meadows, although relatively infrequent on passes, occur on flat areas underlain by sporadic permafrost (Ives 1974). These areas are often adjacent to small ponds. Dominants include *Caltha leptosepala*, *Carex scopulorum*, *C. nigricans*, and *Juncus drummondii*. This same community type in basins usually is adjacent to ponds, lakes, or drainages. *Carex scopulorum*, *Caltha leptosepala*, *Carex*

nigricans, and *Deschampsia caespitosa* are the most frequent dominants. There is a conspicuous difference in species richness between wet meadow hummock communities. Because of the persistence of old leaf bases in hummocks dominated by *Carex scopulorum*, virtually no other taxa can compete. Hummocks dominated by *Carex nigricans* are moderately species-rich.

Shrub tundra. Shrub tundra is far more extensive in the Sawatch Range, than in other mountain ranges studied (Rottman and Hartman 1985, Hartman and Rottman 1985a, 1987), often to the extent that almost the entire basin floor is covered with this community type. *Salix brachycarpa* and *S. glauca* subsp. *glauca* var. *villosa* dominate in drier or well-drained areas on both passes and in basins where they are associated with dry or moist meadow herbaceous understory taxa. *Salix planifolia* is dominant primarily in hydric sites, especially in basins where it may be co-dominant with *Betula glandulosa*. Wet and moist meadow herbaceous taxa are associated with these stands. Basin elevations for shrub tundra were observed from 3538–3904 m.

Krummholz community. The krummholz community type occurs as isolated patches or cushions primarily on slopes of both passes and basins. The overwhelming dominant is *Picea engelmannii*; however, *Pinus aristata* is found on Cumberland Pass and *Pinus contorta* var. *latifolia* occurs in Peekaboo Basin. The herbaceous understory component of this community is represented by both alpine and subalpine taxa. The latter are able to extend into the tundra in this community type because of the greater snow accumulation particularly on the leeward side of the cushion and the lower evapotranspiration rate as a result of overstory shading during the growing season.

Fellfield community. Fellfield community sites are characterized by a high proportion of finely-weathered rock material (up to 80%), coarse-textured soils, and little organic material (Willard 1963). Fellfield communities are far more prevalent on the passes where *Paronychia pulvinata*, *Trifolium nanum*, *Minuartia obtusiloba*, and *Silene acaulis* var. *subacaulescens* form the dominants. This community type in the basins is found primarily on wind-swept ridges. The dominants listed for the passes also occur in the basins; however, *Dryas octopetala* var. *hookeriana* is the most frequent dominant in the latter. The typical cushion plant-dominated fellfield communities found in the Sawatch Range are similar to those of the Front Range (Komarkova 1976, Eddleman and Ward 1984). In the Mosquito Range this community type appears to be restricted to mountain tops and wind-swept ridges (Hartman and Rottman 1985a). In the east-west-trending mountains of the state, the Elk Mountains

(Langenheim 1962), West Elk Mountains (Hartman and Rottman 1987), and San Juan Mountains (Webber et al. 1976, Hartman and Rottman 1985b), this community type is poorly represented.

Rock-predominating community types. Bedrock ledges, rock crevices, and talus habitats are combined into one category of minor importance in terms of community development. Composed of either fractured bedrock outcrops or talus, these habitats are characterized by minimal soil accumulation available for the growth of vascular plant taxa. As a result, community structure is replaced by a diverse assortment of various opportunistic taxa that can tolerate the limitations of the habitat substrates. In some instances, however, bedrock outcrops in the basins are capped by krummholz or dry meadow communities.

Rivulet community. Small rivulets converge to form the major drainages of most basins. Taxa bordering the rivulets are primarily subalpine plants capable of extending upward to high elevations in the tundra because of enhanced moisture availability. Some of the subalpine taxa that can dominate rivulet communities are *Senecio triangularis*, *Aconitum columbianum*, *Cardamine cordifolia*, *Mimulus guttatus*, and *Saxifraga odontoloma*. Shrub tundra communities often border the rivulets.

Snowbank community. Snowbanks may persist late into August in the basins. These areas are subject to shortened growing seasons, often permitting only vegetative growth of taxa found in the area in front of the receding snowbank. *Carex pyrenaica* is a good indicator dominant of this community type. Other taxa worthy of note are *Ranunculus adoneus*, *Sibbaldia procumbens*, and *Salix arctica*. *Carex incurviformis* appears to be restricted to this community. A widespread early-melting snowbank community dominated by *Vaccinium caespitosum*, *Carex pyrenaica*, and *Stereocaulon* sp. assumes a deceptively dry appearance as the season progresses.

FLORA

Comparative floristics. The alpine flora of the Sawatch Range consists of 289 taxa representing 109 genera of angiosperms, four genera and five species of gymnosperms, and five genera and five species of pteridophytes. Our total of 289 taxa compared to the estimated 300 vascular plant taxa in the alpine tundra of Colorado (Bliss 1962) attests to the thoroughness of this study in the Sawatch Range. The largest family is Asteraceae with 47 taxa, followed by Cyperaceae, Poaceae, Brassicaceae, Ranunculaceae, Caryophyllaceae, Rosaceae, and Scrophulariaceae with 34, 23, 21, 16, 15, 14, and 14 taxa, respectively. Comparing these leading families with those of other Colorado alpine floras, the greatest similarity is to the Mosquito

Range to the east (Hartman and Rottman 1985a), the only difference being the addition of Ranunculaceae which exceeds Rosaceae and Scrophulariaceae in the Sawatch alpine. In the Ruby Range of the West Elk Mountains (Hartman and Rottman 1987), San Juan Mountains (Hartman and Rottman 1985b), and Indian Peaks area of the Front Range (Komarkova 1976), Saxifragaceae is among the leading families. Similarities between alpine floristic inventories of the Sawatch Range and the above ranges were analyzed by using Sorensen's Index of Similarity (Mueller-Dombois and Ellenberg 1974). The greatest similarity, 73.3%, again occurs between the Sawatch and Mosquito ranges; however, similarities to the West Elk (73.1%), Indian Peaks area of the Front Range (72.6%), and San Juan Mountains (72.5%) show an overall consistency among the tundra floras of the various ranges. Differences between the inventories at the individual taxon level are in many cases striking, and relate primarily to apparent distributional ranges of the plants or to substrate and microenvironmental dissimilarities.

Rare taxa with restricted occurrences in the Colorado tundra may reflect local environmental conditions or distributional ranges. The following taxa in the Sawatch Range are considered rare or infrequent by Weber (1987): *Anemone parviflora*, *Asplenium viride*, *Astragalus aboriginum*, *Carex arctogena*, *Draba streptobrachia*, *Gentianella tenella*, *Physaria alpina*, *Ranunculus pygmaeus* var. *pygmaeus*, *Saxifraga adscendens* subsp. *oregonensis*, and *Ligularia taraxacoides*. From our experiences in the various tundras of the state we would add *Arabis lemmonii*, *Astragalus molybdenus*, *Draba incerta*, *Erigeron vagus*, and *Ligularia porteri* to this list. *Carex vernacula*, *Erigeron grandiflorus*, and *Ligularia soldanella*, all of which Weber (1987) considers rare, are infrequent in the Sawatch Range. Two new state records recently were reported for the Sawatch Range from Mt. Champion basin. These are *Draba apiculata* var. *apiculata* (Price et al. 1985) and *Antennaria aromatica* (O'Kane et al. 1988).

Phenology. Our 1986 field season extended from 10 June through 10 October, and permitted some interesting phenological observations. Complete snow release in a fellfield on Independence Pass was observed 11 June with 14 taxa in prime anthesis while all other communities on the pass were snow-covered. By 2 July the pass was completely snow-free and vegetative growth was in progress. *Thlaspi montanum* var. *montanum* and *Smelowskia calycina* var. *americana* (fellfield constituents) were in fruit on 10 July. By 5 September this pass and all others were showing the typical reddish-brown coloration of autumn. In the basins, however, a number of extremely dwarfed moist meadows, dominated by *Geum rossii* var. *turbinatum*, *Sibbaldia procumbens*, and *Erigeron melanocephalus*, often found

adjacent to talus or at the interface of slopes and basin floor were in prime anthesis in late August and early September. Ronning (1968) and Owen (1976) have suggested that both stature and late anthesis may relate to either cold soil temperatures or late snow release. On 10 September the entire range was blanketed by the first snow. Seasonal snow accumulations were in evidence by 3 October. At this time some snow depth measurements were made on Independence Pass in communities studied earlier in the season. Even at this early date it was possible to correlate relative snow accumulation, wind patterns of snow distribution, and community types. Snow depths ranged from 2.4–12.6 cm in fellfield communities to a maximum of 10.7–30.0 cm in moist meadows. Shrub tundra communities were intermediate with 12.6 cm on the windward side and 20.8 cm on the leeward side. Obviously these values cannot reflect the total snow accumulation that will occur; however, we feel that the relative ratios of snow depth to community type are maintained throughout the winter and spring seasons.

Calcareous substrates. Although the Sawatch Range is primarily metamorphic in composition, three of our study areas contain localized occurrences of limestone and dolomite. The following taxa were found only on these calcareous substrates: *Anemone parviflora*, *Asplenium viride*, *Astragalus aboriginum*, *A. molybdenus*, *Juncus albescens*, *J. castaneus*, *Ligularia taraxacoides*, *Oreochrysum parryi*, *Oxytropis podocarpa*, *O. viscida*, *Physaria alpina*, *Potentilla ovina*, *Pyrrocoma uniflora*, and *Senecio canus*. Some of these taxa were reported also for limestone substrates in the Mosquito Range (Hartman and Rottman 1985a), Elk Mountains (Langenheim 1962), and Montana (Bamberg and Major 1968). Schroeter (1926), Nordhagen (1955), Curry (1962), and Bamberg and Major (1968) consider *Dryas octopetala* var. *hookeriana* to be an indicator of calcareous rock or soil, but Murdock (1951), Johnson and Billings (1962), and Willard (1963) fail to substantiate this substrate specificity. In the Sawatch Range the occurrence of *Dryas octopetala* var. *hookeriana* does not appear to be substrate specific and, as suggested by Willard (1963), the var. *hookeriana* may be a Southern Rocky Mountain ecotype with low calcium requirements. As previously mentioned, shrub tundra forms extensive stands both on passes and in basins in the range; however, in our calcareous study sites this community type is extremely limited, perhaps reflecting the porosity and downward percolation of water characteristic of limestone-dolomite areas.

Phytogeography. Table 2 shows the phytogeographic distribution of the alpine flora of the Sawatch Range compared to other ranges in Colorado. Four elements are recognized, each of which may be combined with more specific geographical subelements (Komarkova

TABLE 2. COMPARISON OF THE ALPINE FLORA AND GEOGRAPHIC SUBELEMENTS IN THE SAWATCH RANGE WITH OTHER MOUNTAIN RANGES IN COLORADO. Unit abbreviations are cited in the annotated checklist. ¹Hartman and Rottman (1985a), ²Hartman and Rottman (1985b), ³Hartman and Rottman (1987), ⁴Komarkova (1976).

Element	Abbreviation	Sawatch Range	Mosquito ¹ Range	San Juan ² Mountains	West Elk ³ Mountains	Indian Peaks ⁴ Front Range
Boreal montane	BM	25.6%	18.3%	19.8%	24.1%	27.5%
Montane	M	11.4	8.4	6.0	16.8	2.4
Arctic alpine	AA	24.9	30.6	31.5	23.6	28.7
Alpine	A	38.1	42.7	42.7	35.5	41.4
Geographic Subelement						
Circumpolar	C	19.4	20.6	22.9	17.7	25.9
North American	NA	13.8	8.9	10.2	12.3	9.6
Western North American	WNA	31.5	30.0	25.9	32.3	28.2
Rocky Mountains	RM	13.1	13.1	13.7	14.5	11.2
Southern Rocky Mountains	SRM	11.4	10.7	11.6	11.8	9.9
Colorado	CO	2.8	4.6	4.1	1.4	3.2
North American-Asiatic	NAA	6.6	11.2	9.6	8.6	10.8
North American-European	NAE	1.4	0.9	2.0	1.4	1.2

1976). The Rocky Mountains subelement includes the Northern Rocky Mountain province south to the Laramie Basin in Wyoming. The Southern Rocky Mountains subelement includes southern Wyoming, Colorado, New Mexico, and Arizona. The Colorado subelement contains taxa endemic to Colorado. Phytogeographic determinations for taxa are based upon distributions given by Porsild (1957), Weber (1965), Munz and Keck (1970), Komarkova (1976), Cronquist et al. (1977), Porsild and Cody (1980), and Moss (1983).

The largest part of the vascular flora of the Sawatch Range is made up of Alpine (38.1%) and Western North American (31.5%) taxa. The Circumpolar subelement (19.4%), which is primarily linked with the Arctic-Alpine element, is another important component of the flora. The North American-Asiatic subelement (6.6%), although smaller in the Sawatch Range than in the other ranges compared, still indicates a stronger affinity to the Asiatic alpine flora than to the European alpine flora. The Alpine element is consistently the highest in all ranges compared, with the Arctic-Alpine element second in all but the Sawatch Range and West Elk Mountains where the Boreal-Montane is better represented. The proximity of the Mosquito Range to the Sawatch Range makes comparisons of these two particularly significant. For the most part there is a greater correlation between subelements of the two than between elements.

Colorado endemics found in this study include *Alsinanthe macrantha*, *Draba streptobrachia*, *Ligularia soldanella*, *Luzula subcapitata*, *Penstemon hallii*, *P. harbourii*, *Physaria alpina*, and *Potentilla subjuga* var. *subjuga*. Fewer Colorado endemics occur in the Sawatch Range than in the more northerly Indian Peaks area, and in the Mosquito Range, which is due east of the northern part of the Sawatch.

ANNOTATED CATALOGUE OF VASCULAR PLANT TAXA

The terms used in the annotated catalogue to describe occurrence/abundance are a combination of abundance classes and constancy values. In estimating abundance, standard abundance classes were used: very abundant, abundant, frequent, occasional, and rare (Daubenmire 1968). As data from multiple samples of a particular community type accumulated, it was possible to analyze the inventoried taxa and their abundance ratings on the basis of constancy of occurrence between samples of communities. The percentage values of the constancy classes used were taken from Mueller-Dombois and Ellenberg (1974): very abundant (81–100% constancy), abundant (60.1–80% constancy), frequent (40.1–60% constancy), occasional (20.1–40% constancy), and rare (1.5–20% constancy). The abbreviations used for community types for each taxon are: dry meadow (dm); moist meadow (mm); wet meadow (wm); shrub tundra (st);

krummholz (kr); fellfield (ff); rock-predominating including bedrock ledges, rock crevices, and talus (rp); rivulet (rv); and snowbank (sn). In the phytogeographic citation for each taxon, the element precedes the subelement, the two being separated by a slash (Table 2). Bracketed nomenclature follows Weber (1987) and Wittmann et al. (1988). Twenty-two taxa that are indicated by an asterisk (*) after the authority are not found in Nelson and Hartman (1987) and follow the nomenclature of W. A. Weber (1987) and Wittmann et al. (1988).

PTEROPHYTA

Selaginellaceae

Selaginella densa Rydb. var. *densa*. Abundant; dm, mm, st, kr, ff, rp, sn; A/WNA.

Adiantaceae

Cryptogramma acrostichoides R. Br. Rare; rp; BM/NAA.

Aspleniaceae

Asplenium viride Huds. [*A. trichomanes-ramosum* L.]. Rare; rp; AA/C.

Cystopteris fragilis (L.) Bernh. var. *fragilis*. Occasional; st, rp; AA/C.

Woodsia oregana D. C. Eat. var. *oregana*. Occasional; dm, rp; BM/NA.

CONIFEROPHYTA

Cupressaceae

Juniperus communis L. var. *depressa* Pursh [*J. communis* L. subsp. *alpina* (Neilr.) Celak.]. Rare; kr; BM/C.

Pinaceae

Abies lasiocarpa (Hook.) Nutt. var. *lasiocarpa*. Rare; kr; BM/WNA.

Picea engelmannii Parry ex Engelm. Occasional; kr; BM/WNA.

Pinus aristata Engelm.* Rare; kr; BM/WNA.

Pinus contorta Dougl. ex Loud. var. *latifolia* Engelm. ex Wats. [*P. contorta* Dougl. subsp. *latifolia* (Engelm.) Critch.]. Rare; kr; BM/WNA.

ANTHOPHYTA—DICOTYLEDONEAE

Adoxaceae

Adoxa moschatellina L. Rare; mm; BM/C.

Apiaceae

Angelica grayi (Coul. & Rose) Coul. & Rose. Frequent; dm, mm, st, rp; A/SRM.

Cymopterus lemmonii (Coul. & Rose) Dorn [*Pseudocymopterus montanus* (A. Gray) Coul. & Rose]. Occasional; dm, mm, st, kr; M/SRM.

Ligusticum tenuifolium Wats. [*L. filicinum* Wats. var. *tenuifolium* (Wats.) Math. & Const.]. Rare; mm; BM/WNA.

Oreoxis alpina (A. Gray) Coul. & Rose. Very abundant; dm, mm, wm, st, kr, ff, rp, sn; A/SRM.

O. bakeri Coul. & Rose.* Frequent; dm, mm, wm, st, ff, rp; A/SRM.

Oxypolis fendleri (A. Gray) Heller. Rare; rv; M/SRM.

Podistera eastwoodiae (Coul. & Rose) Math. & Const.* Rare; dm; A/SRM.

Asteraceae

- Achillea millefolium* L. var. *lanulosa* (Nutt.) Piper [*A. lanulosa* Nutt.]. Frequent; dm, mm, wm, st, kr, ff, rp; A/WNA.
- Agoseris aurantiaca* (Hook.) Greene var. *aurantiaca*. Occasional; dm, mm, rp; BM/WNA.
- A. glauca* (Pursh) Raf. var. *dasycephala* (Torr. & A. Gray) Jeps. Rare; dm; M/WNA.
- A. glauca* (Pursh) Raf. var. *laciniata* (D. C. Eat.) Smiley. Occasional; dm, mm, kr; BM/NA.
- Antennaria aromatica* Evert. Rare; ff; M/RM. #6671/2942 COLO.
- A. media* Greene. Abundant; dm, mm, wm, st, kr, ff, rp, sn; AA/NAE.
- A. rosea* Greene. Occasional; mm, st, kr; BM/NA.
- A. umbrinella* Rydb. Rare; dm; A/WNA.
- Arnica cordifolia* Hook. Rare; rp; BM/WNA.
- A. mollis* Hook. Rare; mm, rp; BM/NA.
- A. rydbergii* Greene. Occasional; dm, kr; BM/WNA.
- Artemisia campestris* L. subsp. *borealis* (Pall.) Hall & Clem. var. *borealis*. Occasional; dm, mm, kr, ff, rp; AA/C.
- A. scopulorum* A. Gray. Very abundant; dm, mm, wm, st, kr, ff, rp, sn; A/RM.
- Chaenactis alpina* (A. Gray) Jones. Occasional; ff, rp; M/WNA.
- Cirsium scopulorum* (Greene) Ckll. Occasional; dm, rp; A/RM.
- C. tweedyi* (Rydb.) Petr. Occasional; mm, wm, rp; BM/NA.
- Erigeron compositus* Pursh. Occasional; dm, rp; BM/NA.
- E. coulteri* Porter. Rare; dm; BM/WNA.
- E. grandiflorus* Hook. Occasional; dm, mm, st, sn; AA/WNA.
- E. leiomerus* A. Gray. Occasional; dm, mm, ff, rp; M/RM.
- E. melanocephalus* (A. Nels.) A. Nels. Abundant; dm, mm, wm, rp, sn; A/SRM.
- E. peregrinus* (Banks ex Pursh) Greene subsp. *callianthemus* (Greene) Cronq. var. *callianthemus* [*E. peregrinus* (Banks ex Pursh) Greene subsp. *callianthemus* (Greene) Cronq.]. Occasional; dm, mm, wm, st, kr; BM/WNA.
- E. pinnatisectus* (Gray) A. Nels. Abundant; dm, mm, st, ff, rp; A/SRM.
- E. simplex* Greene. Very Abundant; dm, mm, wm, st, kr, ff, rp, sn; A/WNA.
- E. ursinus* D. C. Eat. Rare; dm; M/WNA.
- E. vagus* Pays.* Rare; dm; A/WNA.
- Haplopappus pygmaeus* (Torr. & A. Gray) A. Gray [*Tonestus pygmaeus* (Torr. & A. Gray) A. Nels.]. Frequent; dm, kr, ff, rp; A/RM.
- Heterotheca fulcrata* (Greene) Shinn. Occasional; dm, rp; M/RM.
- Hieracium gracile* Hook. var. *gracile* [*Chlorocrepis tristis* (Willd. ex Spreng.) A. Löve & D. Löve subsp. *gracile* (Hook.) W. A. Weber]. Occasional; dm, mm, st, rp; A/WNA.
- Hymenoxys grandiflora* (Torr. & A. Gray ex A. Gray) K. Parker [*Rydbergia grandiflora* (Torr. & A. Gray) Greene]. Frequent; dm, mm, st, kr, ff, rp; A/RM.
- Ligularia amplexans* (A. Gray) W. A. Weber.* Occasional; mm, wm, rp; M/RM.
- L. holmii* (Greene) W. A. Weber.* Abundant; dm, mm, ff, rp, sn; A/RM.
- L. porteri* (Greene) W. A. Weber.* Rare; rp; A/RM.
- L. soldanella* (A. Gray) W. A. Weber. Occasional; ff, rp; A/CO.
- L. taraxacoides* (A. Gray) W. A. Weber.* Rare; rp; A/SRM.
- Oreochrysum parryi* (A. Gray) Rydb.* Rare; dm; M/SRM.
- Pyrrocoma uniflora* (Hook.) Greene. Occasional; dm, mm, st, sn; M/WNA.
- Senecio atratus* Greene. Rare; rp; A/SRM.
- S. canus* Hook. [*Packera cana* (Hook.) W. A. Weber & A. Löve]. Occasional; dm, rp; M/WNA.
- S. crassulus* A. Gray. Occasional; dm, mm, wm, st, rp; BM/WNA.
- S. dimorphophyllus* Greene var. *dimorphophyllus* [*Packera dimorphophylla* (Greene) W. A. Weber & A. Löve]. Frequent; mm, wm, st, rp, rv, sn; M/RM.
- S. fremontii* Torr. & A. Gray var. *blitoides* (Greene) Cronq. [*S. fremontii* Torr. & A. Gray subsp. *blitoides* (Greene) Cronq.]. Occasional; rp; A/SRM.

- S. integerrimus* Nutt. var. *integerrimus*. Occasional; mm; M/WNA.
S. triangularis Hook. Occasional; mm, wm, st, rv; BM/WNA.
S. werneriaefolius (A. Gray) A. Gray [*Packera wernerifolia* (A. Gray) W. A. Weber & A. Löve]. Abundant; dm, mm, kr, ff, rp, sn; A/WNA.
Solidago spathulata DC. var. *nana* (A. Gray) Cronq. Frequent; dm, mm, st, kr, ff, rp; A/WNA.
Taraxacum ceratophorum (Ledeb.) DC. [*T. ovinum* Greene]. Occasional; kr, ff, rp, sn; AA/C.

Betulaceae

- Betula glandulosa* Michx. Occasional; wm, st, kr; BM/NA.

Boraginaceae

- Eritrichium nanum* (Vill.) Schrad. var. *elongatum* (Rydb.) Cronq. [*Eritrichium aretioides* (Cham.) DC.]. Frequent; dm, mm, st, ff, rp; AA/NAA.
Mertensia ciliata (James ex Torr.) G. Don. Occasional; mm, wm, st, rp, rv; BM/WNA.
M. lanceolata (Pursh) A. DC.* Occasional; dm, mm, st; A/SRM.
M. viridis (A. Nels.) A. Nels. [*M. lanceolata* (Pursh) A. DC. var. *viridis* A. Nels.]. Very abundant; dm, mm, wm, st, kr, ff, rp, rv; A/WNA.

Brassicaceae

- Arabis drummondii* A. Gray [*Boechea drummondii* (A. Gray) A. Löve & D. Löve]. Rare; st, kr; BM/NA.
A. lemmonii Wats. [*Boechea lemmonii* (Wats.) W. A. Weber]. Rare; rp; A/WNA.
Cardamine cordifolia A. Gray var. *cordifolia*. Occasional; mm, st, rp, rv; BM/WNA.
Descurainia richardsonii (Sweet) O. E. Schulz var. *richardsonii*. Rare; st, rp; BM/NA.
Draba apiculata C. L. Hitchc. var. *apiculata*. Rare; rp; A/RM. #6025/2296 COLO.
D. aurea Vahl ex Hornem. var. *aurea*. Abundant; dm, mm, st, kr, ff, rp; AA/C.
D. cana Rydb. Occasional; dm, mm, st, rp; AA/C.
D. crassa Rydb. Occasional; rp; A/RM.
D. crassifolia Grah. var. *crassifolia*. Very abundant; dm, mm, wm, st, kr, ff, rp, sn; AA/NAE.
D. fladnizensis Wulf. Rare; dm, st; AA/C.
D. incerta Pays. Rare; rp; A/RM.
D. lonchocarpa Rydb. var. *lonchocarpa*. Frequent; dm, mm, rp; AA/NA.
D. oligosperma Hook. Occasional; dm, mm, rp; AA/WNA.
D. spectabilis Greene var. *spectabilis*. Rare; dm, kr; M/RM.
D. streptobrachia Price. Rare; dm, ff; A/CO.
D. streptocarpa A. Gray var. *streptocarpa*. Occasional; ff, rp; A/SRM.
Erysimum nivale (Greene) Rydb. [*E. capitatum* (Dougl.) Greene]. Frequent; dm, mm, st, ff, rp; A/SRM.
Physaria alpina Roll. Rare; rp; A/CO.
Rorippa curvipes Greene var. *alpina* (Wats.) Stuckey. Rare; wm, rv; A/RM.
Smelowskia calycina (Steph. ex Willd.) C. A. Mey. var. *americana* (Regel & Herd.) Drury & Roll. [*S. calycina* (Steph. ex Willd.) C. A. Mey.]. Abundant; dm, mm, st, kr, ff, rp; AA/NAA.
Thlaspi montanum L. var. *montanum* [*Noccaea montana* (L.) F. K. Mey.]. Very abundant; dm, mm, wm, st, kr, ff, rp, sn; AA/C.

Campanulaceae

- Campanula rotundifolia* L. Rare; dm, rp; BM/C.
C. uniflora L. Frequent; dm, mm, st, ff, rp; A/C.

Caryophyllaceae

- Alsianthe macrantha* (Rydb.) W. A. Weber. Rare; rp; A/CO.
Arenaria congesta Nutt. var. *congesta* [*Eremogone congesta* (Nutt. ex Torr. & A. Gray) Ikonn.]. Occasional; dm, rp; M/WNA.
A. fendleri A. Gray var. *fendleri* [*Eremogone fendleri* (A. Gray) Ikonn.]. Abundant; dm, mm, st, kr, ff, rp; A/SRM.
Cerastium arvense L. [*Alsine media* L.]. Occasional; dm, mm, st, ff, rp; BM/C.
C. beeringianum Cham. & Schlecht. [*C. beeringianum* Cham. & Schlecht. subsp. *earlei* (Rydb.) Hulten]. Occasional; dm, rp; A/RM.
Gastrollychnis kingii (Wats.) W. A. Weber.* Rare; dm, rp; A/SRM.
Minuartia austromontana S. J. Wolf & Packer [*Alsianthe stricta* (Sw.) Reichenb.]. Rare; mm, ff, rp; AA/NA.
M. obtusiloba (Rydb.) House [*Lidia obtusiloba* (Rydb.) A. Löve & D. Löve]. Very abundant; dm, mm, st, kr, ff, rp, sn; AA/NAA.
M. rubella (Wahlenb.) Hiern [*Tryphane rubella* (Wahlenb.) Reichenb.]. Frequent; dm, mm, st, ff, rp; AA/C.
Paronychia pulvinata A. Gray. Occasional; dm, ff, rp; A/SRM.
Sagina saginoides (L.) Karst. Frequent; dm, mm, wm, rp, sn; AA/C.
Silene acaulis (L.) Jacq. var. *subacaulescens* (F. N. Williams) Fern. & St. John [*S. acaulis* subsp. *subacaulescens* (F. N. Will.) C. L. Hitchc. & Maguire]. Very abundant; dm, mm, st, kr, rp, sn; AA/NAA.
S. drummondii Hook. var. *drummondii* [*Gastrollychnis drummondii* (Hook.) A. Löve & D. Löve]. Occasional; dm, wm, kr; BM/NA.
Stellaria longipes Goldie var. *longipes*. Frequent; dm, mm, st, kr, rp; BM/NA.
S. umbellata Turcz. ex Kar. & Kir. Frequent; dm, mm, st, rp, sn; A/NAA.

Crassulaceae

- Sedum integrifolium* (Raf.) A. Nels. subsp. *integrifolium* [*Rhodiola integrifolia* Raf.]. Abundant; dm, mm, wm, rp, rv; AA/NAA.
S. lanceolatum Torr. var. *lanceolatum* [*Amerosedum lanceolatum* (Torr.) A. Löve & D. Löve]. Frequent; dm, mm, st, kr, ff, rp; A/RM.
S. rhodanthum A. Gray [*Clementsia rhodantha* (A. Gray) Rose]. Occasional; mm, wm, st, rp, rv; A/RM.

Ericaceae

- Arctostaphylos uva-ursi* (L.) Spreng. subsp. *uva-ursi* [*A. adenotricha* (Fern. & Macbr.) A. Löve, D. Löve & Kapoor]. Rare; dm, st; BM/NA.
Gaultheria humifusa (Grah.) Rydb. Rare; mm; BM/WNA.
Kalmia microphylla (Hook.) Heller var. *microphylla*. Rare; wm; BM/WNA.
Vaccinium caespitosum Michx. [*V. cespitosum* Michx.]. Very abundant; dm, mm, wm, st, kr, rp, sn; BM/NA.
V. myrtillus L. subsp. *oreophilum* (Rydb.) A. Löve, D. Löve & Kapoor. Rare; dm, mm, rp; BM/C.
V. scoparium Leib. ex Cov. Rare; kr; BM/WNA.

Fabaceae

- Astragalus aboriginum* Richards. Rare; dm; BM/WNA.
A. molybdenus Barneby.* Rare; dm; AA/C.
A. tenellus Pursh. Rare; dm, mm; BM/WNA.
Oxytropis deflexa (Pall.) DC. var. *sericea* Torr. & A. Gray. Occasional; dm, mm, st, rp; BM/C.
O. parryi A. Gray. Rare; st; A/WNA.
O. podocarpa A. Gray. Occasional; dm, ff, rp; AA/C.
O. sericea Nutt. var. *sericea*. Rare; dm, st; BM/NA.
O. viscida Nutt. var. *viscida*. Rare; mm; A/WNA.

Trifolium dasyphyllum Torr. & A. Gray var. *dasyphyllum*. Abundant; dm, mm, st, kr, ff, rp; A/RM.

T. nanum Torr. Abundant; dm, mm, st, kr, ff, rp; A/RM.

T. parryi A. Gray var. *parryi*. Frequent; dm, mm, wm, st, rp; A/RM.

Gentianaceae

Frasera speciosa Dougl. ex Griseb. Rare; dm; BM/WNA.

Gentiana algida Pall. [*Gentianodes algida* (Pall.) A. Löve & D. Löve]. Occasional; dm, mm, st; AA/NAA.

G. calycosa Griseb. [*Pneumonanthe parryi* (Engelm.) Greene]. Rare; dm, mm; A/WNA.

G. prostrata Haenke ex Jacq. [*Chondrophylla prostrata* (Haenke ex Jacq.) J. P. Anders.]. Occasional; dm, mm, st; AA/NAA.

Gentianella amarella (L.) Borner [*G. acuta* (Michx.) Hiit.]. Occasional; dm, mm, st, ff, rp; BM/C.

G. tenella (Rottb.) Borner [*Comastoma tenellum* (Rottb.) Toyokuni]. Rare; mm; AA/C.

Gentianopsis barbellata (Engelm.) Iltis. Rare; dm, ff; A/SRM.

G. detonsa (Rottb.) Ma var. *elegans* (A. Nels.) N. Holmgren [*G. thermalis* (Kuntze) Iltis]. Occasional; mm; A/RM.

Swertia perennis L. Occasional; mm, wm, st; A/C.

Grossulariaceae

Ribes montigenum McClat. Occasional; st, kr, rp; BM/WNA.

Hydrophyllaceae

Phacelia glandulosa Nutt. Rare; rp; BM/WNA.

P. hastata Dougl. ex Lehm. var. *hastata*. Rare; dm, rp; M/NA.

P. sericea (Grah. ex Hook.) A. Gray var. *sericea*. Frequent; dm, mm, st, kr, ff; A/WNA.

Onagraceae

Epilobium anagallidifolium Lam. Frequent; wm, st, rp, rv, sn; AA/C.

E. hornemannii Reichenb. subsp. *hornemannii*. Rare; wm, st; AA/C.

Polemoniaceae

Phlox pulvinata (Wherry) Cronq. [*P. condensata* (A. Gray) E. Nels.]. Abundant; dm, st, ff, rp; A/SRM.

Polemonium pulcherrimum Hook. var. *pulcherrimum* [*P. pulcherrimum* Hook. subsp. *delicatum* (Rydb.) Brand]. Rare; st, kr; M/SRM.

P. viscosum Nutt. Abundant; dm, mm, st, kr, ff, rp; A/WNA.

Polygonaceae

Eriogonum jamesii Benth. var. *xanthum* (Stokes) Reveal.* Rare; dm, st; A/WNA.

Oxyria digyna (L.) Hill. Frequent; mm, rp, rv; AA/C.

Polygonum bistortoides Pursh [*Bistorta bistortoides* (Pursh) Small]. Very abundant; dm, mm, wm, st, kr, ff, rp; A/WNA.

P. douglasii Greene var. *douglasii*. Rare; ff; BM/NA.

P. viviparum L. var. *viviparum* [*Bistorta vivipara* (L.) S. Gray]. Abundant; dm, mm, wm, st, kr, ff, rp; AA/C.

Portulacaceae

Claytonia megarhiza (A. Gray) Parry ex Wats. var. *megarhiza* [*C. megarhiza* (Parry ex A. Gray) Wats.]. Frequent; ff, rp; A/RM.

Lewisia pygmaea (A. Gray) B. L. Robins. [*Oreobroma pygmaea* (A. Gray) Howell].
Frequent; dm, mm, st, kr, rp, sn; A/WNA.

Primulaceae

Androsace septentrionalis L. Abundant; dm, mm, wm, st, kr, ff, rp; AA/C.

Primula angustifolia Torr.* Frequent; dm, mm, ff, rp, sn; A/SRM.

P. parryi A. Gray. Frequent; mm, wm, rp, rv, sn; A/RM.

Ranunculaceae

Aconitum columbianum Nutt. var. *columbianum*. Rare; mm, rv; BM/WNA.

Anemone multifida Poir. var. *multifida* [*A. multifida* Poir. var. *globosa* (Nutt.) Torr. & A. Gray]. Occasional; dm, st, kr, rp; BM/NA.

A. narcissiflora L. subsp. *zephyra* (A. Nels.) A. Löve, D. Löve & Kapoor [*Anemonastrum narcissiflorum* (L.) Holub. subsp. *zephyrum* (A. Nels.) W. A. Weber]. Frequent; dm, mm, wm, st, kr, ff, sn; A/SRM.

A. parviflora Michx. Rare; mm, rp; BM/NAA.

A. patens L. [*Pulsatilla patens* (L.) Mill. subsp. *multifida* (Pritz.) Zamels]. Rare; rp; BM/NA.

Aquilegia caerulea James. Frequent; dm, mm, st, kr, rp; M/RM.

Caltha leptosepala DC. subsp. *leptosepala* var. *leptosepala* [*Psychrophila leptosepala* (DC.) W. A. Weber]. Occasional; mm, wm, st, rv, sn; A/WNA.

Delphinium barbeyi (Huth) Huth. Rare; mm; M/SRM.

Ranunculus adoneus A. Gray. Infrequent; mm, sn; A/WNA.

R. eschscholtzii Schlecht. var. *eschscholtzii*. Frequent; dm, mm, wm, rp, rv, sn; AA/NAA.

R. inamoenus Greene var. *alpeophilus* (A. Nels.) Benson [*R. inamoenus* Greene]. Rare; mm; M/WNA.

R. macauleyi A. Gray.* Rare; mm; A/SRM.

R. pedatifidus J. E. Sm. var. *affinis* (R. Br.) Benson [*R. pedatifidus* J. E. Sm.]. Rare; dm; AA/C.

R. pygmaeus Wahlenb. var. *pygmaeus*. Rare; wm; AA/C.

Thalictrum alpinum L. var. *hebetum* Boivin [*T. alpinum* L.]. Frequent; dm, mm, wm, st, rp, sn; A/WNA.

Trollius laxus Salisb. [*T. albiflorus* (A. Gray) Rydb.]. Occasional; mm, st; BM/WNA.

Rosaceae

Dryas octopetala L. var. *hookeriana* (Juz.) Breit. [*D. octopetala* L. subsp. *hookeriana* (Juz.) Hulten]. Frequent; dm, mm, st, kr, ff, rp; A/RM.

Fragaria vesca L. var. *bracteata* (Heller) R. J. Davis [*F. vesca* L. subsp. *bracteata* (Heller) R. J. Davis]. Rare; dm, kr; BM/NA.

Geum rossii (R. Br.) Ser. var. *turbinatum* (Rydb.) C. L. Hitchc. [*Acomastylis rossii* (R. Br.) Greene subsp. *turbinata* (Rydb.) W. A. Weber]. Very abundant; dm, mm, wm, st, kr, ff, rp, rv, sn; AA/NA.

Potentilla concinna Richards. var. *concinna*. Rare; dm, st; M/WNA.

P. diversifolia Lehm. var. *diversifolia*. Very abundant; dm, mm, wm, st, kr, ff, rp, sn; A/WNA.

P. fruticosa L. [*Pentaphylloides floribunda* (Pursh) A. Löve]. Occasional; dm, st, rp; BM/C.

P. hookeriana Lehm. subsp. *hookeriana* var. *hookeriana* [*P. hookeriana* Lehm.]. Frequent; dm, st, ff, rp; AA/NAA.

P. nivea L. Occasional; dm, ff, rp; AA/C.

P. ovina Macoun var. *decurrens* (Wats.) Welsh & B. C. Johnston. Rare; dm; M/RM.

P. ovina Macoun var. *ovina*. Rare; dm; M/WNA.

P. pulcherrima Lehm. Occasional; dm, mm, st, ff, rp; BM/WNA.

P. rubricaulis Lehm. Occasional; dm, kr, ff, rp; AA/NA.

P. subjuga Rydb. var. *subjuga*. Frequent; dm, ff, rp; A/CO.

Sibbaldia procumbens L. Abundant; dm, mm, wm, st, rp, sn; AA/C.

Salicaceae

Salix arctica Pall. [*S. arctica* Pall. subsp. *petraea* (Anderss.) A. Löve, D. Löve & Kapoor]. Abundant; dm, mm, wm, st, ff, rp, sn; A/WNA.

S. brachycarpa Nutt. subsp. *brachycarpa* var. *brachycarpa* [*S. brachycarpa* Nutt.]. Frequent; dm, mm, st, kr, rp; BM/NA.

S. glauca L. subsp. *glauca* var. *villosa* (Hook.) Anderss. Occasional; mm, st, kr; BM/WNA.

S. planifolia Pursh subsp. *planifolia* var. *planifolia* [*S. planifolia* Pursh]. Occasional; mm, wm, st, ff; BM/NA.

S. reticulata L. subsp. *nivalis* (Hook.) A. Löve, D. Löve & Kapoor. Very abundant; dm, mm, wm, st, kr, ff, rp, sn; A/WNA.

Saxifragaceae

Heuchera parvifolia Nutt. ex Torr. & A. Gray [*H. parvifolia* Nutt. ex Torr. & A. Gray var. *nivalis* (Rosend.) A. Löve, D. Löve & Kapoor]. Abundant; dm, mm, st, kr, ff, rp; M/RM.

Micranthes oregana (Howell) Small.* Occasional; mm, wm, st, rv; M/WNA.

Saxifraga adscendens L. subsp. *oregonensis* (Raf.) Breit. [*Muscaria adscendens* (L.) Small]. Occasional; rp; AA/NAE.

S. brachialis L. subsp. *austromontana* (Wieg.) G. N. Jones [*Ciliaria austromontana* (Wieg.) W. A. Weber]. Frequent; dm, mm, st, kr, ff, rp; A/WNA.

S. caespitosa L. var. *minima* Blank. [*Muscaria delicatula* Small]. Rare; rp; AA/C.

S. cernua L. Occasional; rp; AA/C.

S. debilis Engelm. ex A. Gray [*S. hyperborea* R. Br. subsp. *debilis* (Engelm. ex A. Gray) A. Löve, D. Löve & Kapoor]. Frequent; dm, rp; AA/NA.

S. flagellaris Willd. ex Sternb. subsp. *flagellaris* [*Hirculus platysepalus* (Trautv.) W. A. Weber subsp. *crandallii* (Gand.) W. A. Weber]. Frequent; dm, mm, st, kr, ff, rp; A/SRM.

S. odontoloma Piper [*Micranthes odontoloma* (Piper) Heller]. Occasional; wm, st, rv; BM/WNA.

S. rhomboidea Greene var. *rhomboidea* [*Micranthes rhomboidea* (Greene) Small]. Very abundant; dm, mm, st, kr, ff, rp, rv, sn; A/WNA.

S. rivularis L. var. *flexuosa* (Sternb.) Engl. & Irmsch. [*S. rivularis* L.]. Rare; rp; AA/C.

Scrophulariaceae

Besseyia alpina (A. Gray) Rydb. Frequent; dm, mm, ff, rp; A/SRM.

Castilleja miniata Dougl. ex Hook. Rare; dm, rp; BM/WNA.

C. occidentalis Torr.* Very abundant; dm, mm, wm, st, kr, ff, rp, rv, sn; A/RM.

C. rhexifolia Rydb. Occasional; mm, wm, st, rv; BM/WNA.

Chionophila jamesii Benth. Frequent; dm, mm, ff, rp, sn; A/SRM.

Mimulus guttatus DC. subsp. *guttatus*. Rare; rv; BM/NA.

Pedicularis bracteosa Benth. ex Hook. var. *paysoniana* (Penn.) Cronq. [*P. bracteosa* Benth. subsp. *paysoniana* (Penn.) W. A. Weber]. Rare; st; M/RM.

P. groenlandica Retz. var. *surrecta* (Benth. ex Hook.) A. Gray [*P. groenlandica* Retz.]. Frequent; mm, wm, st, rp, rv, sn; AA/NA.

P. parryi A. Gray subsp. *parryi*. Occasional; dm, mm, st, kr; A/RM.

P. scopulorum A. Gray.* Occasional; mm, wm, st; A/RM.

Penstemon hallii A. Gray. Rare; dm, ff; A/CO.

P. harbourii A. Gray. Rare; rp; A/CO.

P. whippleanus A. Gray. Occasional; st, kr, rp; M/RM.

Veronica nutans Bong.* Frequent; dm, mm, wm, st, kr, rp, rv; AA/NA.

Valerianaceae

Valeriana acutiloba Rydb. var. *acutiloba* [*V. capitata* Pall. ex Link subsp. *acutiloba* (Rydb.) F. G. Mey.]. Rare; dm; AA/NA.

V. edulis Nutt. ex Torr. & A. Gray var. *edulis*. Rare; dm, rp; BM/WNA.

Violaceae

Viola adunca Sm. var. *bellidifolia* (Greene) Harrington [*V. labradorica* Schrank]. Occasional; dm, mm, wm, st, kr, rp; BM/NA.

ANTHOPHYTA—MONOCOTYLEDONEAE

Cyperaceae

Carex albonigra Mack. [*C. albo-nigra* Mack. in Rydb.]. Frequent; dm, mm, wm, st, kr, ff, rp; AA/WNA.

C. aquatilis Wahlenb. var. *aquatilis* [*C. aquatilis* Wahlenb. subsp. *stans* (Drejer) Hulten]. Occasional; mm, wm, rv; AA/C.

C. arapahoensis Clokey.* Rare; dm, mm; A/SRM.

C. arctogena H. Sm. [*C. capitata* L. subsp. *arctogena* (H. Smith) Böcher]. Rare; mm; BM/NA.

C. aurea Nutt. Rare; mm; BM/NA.

C. bipartita Bellardi ex All. var. *bipartita* [*C. lachenalii* Schkuhr]. Rare; mm; AA/C.

C. brevipes W. Boott. Rare; dm, kr; BM/NA.

C. capillaris L. subsp. *capillaris*. Rare; mm; AA/C.

C. ebenea Rydb. Abundant; dm, mm, wm, st, kr, rp, rv, sn; A/RM.

C. elynoides Holm. Very abundant; dm, mm, st, kr, ff, rp, sn; A/WNA.

C. foenea Willd. Occasional; dm, mm, st, kr, ff; BM/NA.

C. haydeniana Olney. Occasional; dm, mm, wm, rp; A/WNA.

C. heteroneura W. Boott var. *chalciolepis* (Holm) F. J. Herm. [*C. chalciolepis* Holm]. Abundant; dm, mm, wm, st, kr, ff, rp, sn; A/WNA.

C. heteroneura W. Boott var. *epapillosa* (Mack.) F. J. Herm. [*C. epapillosa* Mack. in Rydb.]. Rare; dm, mm; M/WNA.

C. illota Bailey. Rare; mm, wm; A/WNA.

C. incurviformis Mack. [*C. maritima* Gunn.]. Rare; rp, sn; A/WNA.

C. missouriensis R. Br. Rare; mm, st; AA/C.

C. nardina Fries var. *hepburnii* (Boott) Kukenth. [*C. nardina* Fries subsp. *hepburnii* (Boott) A. Löve, D. Löve & Kapoor]. Rare; mm, wm; A/SRM.

C. nelsonii Mack. Rare; mm; A/SRM.

C. nigricans C. A. Mey. Frequent; mm, wm, st, rp, rv; AA/NA.

C. norvegica Retz. Rare; dm, mm, rp; AA/NAE.

C. nova Bailey. Frequent; mm, wm, st, rp, rv; BM/WNA.

C. obtusata Lilj. Rare; mm, st; BM/C.

C. pergloboosa Mack.* Rare; rp, sn; A/SRM.

C. phaeocephala Piper. Frequent; dm, mm, st, kr, rp, sn; A/WNA.

C. preceptorum Mack. Rare; mm, wm; A/WNA.

C. pseudoscirpoidea Rydb. Frequent; dm, mm, st, kr, ff, rp; A/WNA.

C. pyrenaica Wahlenb. [*C. praegracilis* Boott]. Occasional; mm, rp, sn; A/C.

C. rupestris All. var. *drummondii* (Dewey) Bailey [*C. rupestris* All. subsp. *drummondiana* (Dewey) Holub]. Frequent; dm, mm, st, kr, ff, rp; A/RM.

C. saxatilis L. [*C. saxatilis* L. subsp. *laxa* (Trautv.) Kalela]. Rare; wm; AA/C.

C. scopulorum Holm var. *scopulorum*. Frequent; mm, wm, st, rp, rv; A/WNA.

C. vernacula Bailey. Occasional; mm, wm, rp, rv; A/WNA.

Eleocharis pauciflora (Lightf.) Link [*E. quinquefolia* (F. X. Hartm.) Schwartz]. Rare; wm; A/C.

Kobresia bellardii (All.) Degl. ex Loisel. [*K. myosuroides* (Vill.) Fiori & Paoli]. Frequent; dm, mm, st, kr, ff, rp; AA/C.

Juncaceae

- Juncus albescens* (Lange) Fern. Rare; mm; AA/NA.
J. balticus Willd. var. *montanus* Engelm. [*J. arcticus* Willd. subsp. *ater* (Rydb.) Hul-
 ten]. Rare; mm; M/WNA.
J. biglumis L. Rare; mm, wm, rp; AA/C.
J. castaneus Sm. subsp. *castaneus* var. *castaneus*. Rare; mm; AA/C.
J. drummondii E. Mey. var. *drummondii*. Very abundant; dm, mm, wm, st, kr, rp,
 rv, sn; A/WNA.
J. mertensianus Bong. Occasional; mm, wm, rv; A/NAA.
J. parryi Engelm. Rare; mm; M/WNA.
J. triglumis L. Rare; mm; AA/C.
Luzula parviflora (Ehrh.) Desv. [*L. parviflora* (Ehrh. ex Hoffm.) Lejeune]. Rare; mm,
 rv; BM/C.
L. spicata (L.) DC. Very abundant; dm, mm, wm, st, kr, ff, rp, sn; A/RM.
L. subcapitata (Rydb.) Harr. Rare; mm, wm; A/CO.

Liliaceae

- Lloydia serotina* (L.) Sweet subsp. *serotina*. Abundant; dm, mm, wm, st, kr, ff, rp,
 sn; AA/C.
Zigadenus elegans Pursh subsp. *elegans* [*Anticlea elegans* (Pursh) Rydb.]. Occasional;
 dm, mm, st, rp; AA/NA.

Poaceae

- Agropyron latiglume* (Scribn. & Sm.) Rydb. [*Elymus trachycaulus* (Link) Gould ex
 Shinnars subsp. *andinus* (Scribn. & Sm.) A. Löve & D. Löve]. Occasional; dm,
 st, rp; AA/NA.
A. scribneri Vasey [*Elymus scribneri* (Vasey) Jones]. Frequent; dm, kr, ff, rp; A/WNA.
Agrostis borealis Hartm. [*A. mertensii* Trin.]. Rare; dm, mm; AA/C.
A. humilis Vasey. Rare; mm, st; A/WNA.
A. variabilis Rydb. Rare; dm; A/WNA.
Calamagrostis canadensis (Michx.) Beauv. Rare; st; BM/NAA.
C. purpurascens R. Br. var. *purpurascens*. Occasional; dm, kr, ff, rp; AA/NAA.
Danthonia intermedia Vasey. Occasional; dm, st, rp; BM/NAA.
Deschampsia caespitosa (L.) Beauv. var. *caespitosa* [*D. caespitosa* (L.) P. Beauv. subsp.
alpicola (Rydb.) A. Löve, D. Löve & Kapoor]. Abundant; dm, mm, wm, st, rp,
 rv, sn; BM/C.
Festuca ovina L. var. *brevifolia* (R. Br.) Wats. [*F. minutiflora* Rydb.]. Very abundant;
 dm, mm, wm, st, kr, ff, rp, sn; AA/C.
F. ovina L. var. *rydbergii* St. Yves [*F. brachyphylla* subsp. *coloradensis* Fred.]. Oc-
 casional; dm, st, kr, ff; M/NA.
Helictotrichon mortonianum (Scribn.) Henr. Occasional; dm, mm, ff, rp; A/SRM.
Phleum alpinum L. [*P. commutatum* Gaud.]. Frequent; dm, mm, wm, st, rp, sn;
 AA/C.
Poa alpina L. var. *alpina*. Abundant; dm, mm, wm, st, kr, rp, sn; AA/C.
P. cusickii Vasey. Rare; dm; M/RM.
P. epilis Scribn. [*P. cusickii* Vasey subsp. *epilis* (Scribn.) W. A. Weber]. Frequent;
 dm, mm, wm, st, kr, rp; BM/WNA.
P. fendleriana (Steud.) Vasey. Occasional; dm, mm, st; BM/NA.
P. grayana Vasey [*P. arctica* R. Br.]. Occasional; dm, mm, st, rp; A/RM.
P. interior Rydb. [*P. nemoralis* L. subsp. *interior* (Rydb.) W. A. Weber]. Rare; dm;
 BM/NA.
P. reflexa Vasey & Scribn. ex Vasey. Occasional; mm, st, kr; A/WNA.
P. rupicola Nash ex Rydb. [*P. glauca* M. Vahl subsp. *rupicola* (Nash) W. A. Weber].
 Abundant; dm, mm, st, kr, ff, rp; A/WNA.

- P. sandbergii* Vasey [*P. secunda* C. Presl]. Rare; dm, mm; BM/NA.
Trisetum spicatum (L.) Richt. var. *spicatum* [*T. spicatum* (L.) Richt. subsp. *congdonii* (Scribn. & Merr.) Hulten]. Very abundant; dm, mm, wm, st, kr, ff, rp, sn; AA/C.

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ERRATUM

Part of the address of Mountain West Publishing was inadvertently omitted when the announcement below appeared in *Madroño* 35(2):125. The announcement is repeated here with the complete address.

ANNOUNCEMENT

New Publication

DORN, ROBERT D. 1988. *Vascular Plants of Wyoming*, illustrated by JANE L. DORN. Mountain West Publishing, Cheyenne, WY. vi + 340 pp., paperbound. [Keys to 120 families, 650 genera, 2369 species, 39 subspecies, and 690 varieties; 93 new combinations, 1 new species, 4 new varieties, and 1 new name; section of taxonomic notes. Available postpaid for \$13.00 from Mountain West Publishing, Box 1471, Cheyenne, WY 82003.]

ANNOUNCEMENT

NEW PUBLICATION

POWELL, A. M. 1988. *Trees and Shrubs of Trans-Pecos Texas*, Big Bend Natural History Association, P.O. Box 68, Big Bend National Park, TX 79834, 536 pp., illus., ISBN 0-912001-14-3, \$19.95 (paperbound). Includes keys, descriptions, distributions, and illustrations of about 450 species of woody plants native to the Texas mountain and desert region west of the Pecos River. (Also available, Chihuahuan Desert Research Institute, P.O. Box 1334, Alpine, TX 79831, \$17.95 to members, \$19.95 to non-members.)

LATE WISCONSIN VEGETATION OF ROBBER'S ROOST IN THE WESTERN MOJAVE DESERT, CALIFORNIA

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ABSTRACT

A total of 22 plant taxa were identified from three packrat (*Neotoma* sp.) midden assemblages radiocarbon dated at 12,870–13,330 yr B.P. at 1215 m elevation in Robber's Roost in the Scodie Mountains of Kern Co., California. The Late Wisconsin vegetation was a pinyon-juniper woodland dominated by *Pinus monophylla*, *Juniperus californica*, and *Ceanothus greggii*. Excellent modern analogs are in Cushenberry Canyon and similar areas on the desert slopes of the San Bernardino and San Gabriel mountains. These woodlands are probably relicts of a pinyon-juniper-Joshua tree woodland that was widespread across the southern Mojave Desert in the Late Wisconsin.

Plant macrofossils from ancient packrat (*Neotoma* sp.) middens have provided a detailed record of the invasion of the present deserts of North America by woodland or forest trees (Van Devender and Spaulding 1979). Woodlands dominated by *Pinus monophylla*, *Juniperus osteosperma*, and *Yucca brevifolia* were present in many parts of the present Mojave Desert in southern Nevada (Wells and Berger 1967, Leskinen 1975, Spaulding 1981) and southeastern California (Mehring 1965, Wells and Berger 1967, King 1976, Wells and Woodcock 1985). Characteristic dominants of the modern Mojave desertscrub such as *Larrea divaricata* and *Ambrosia dumosa* were noticeably absent from these areas. In this paper, we present the first analyses of Late Wisconsin packrat midden plant assemblages from the base of the Sierra Nevada on the western edge of the Mojave Desert and discuss their local and regional implications.

STUDY AREA

The Scodie Mountains are on the southeastern end of the Sierra Nevada in Kern Co., California (Fig. 1). They range from 1160 m elevation on the southeastern base to 2075 m on Pinyon Peak and 2170 m on Skinner Peak. The upper portion of the range is in Sequoia National Forest. Walker Pass at 1905 m in Freeman Canyon marks the northeastern edge of the range. The Scodie Mountains divide

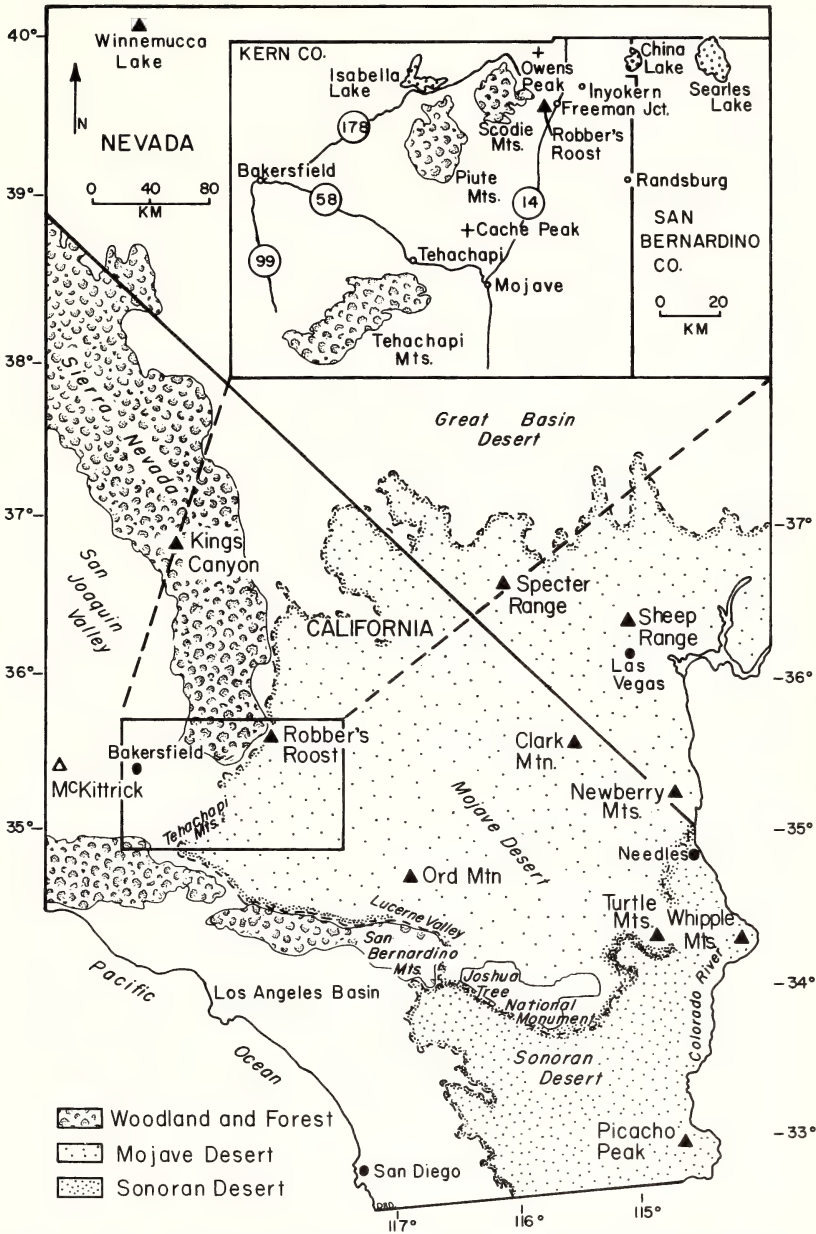


FIG. 1. Map of southern California showing the location of Robber's Roost in the Mojave Desert and in relation to the Sierra Nevada and other fossil packrat midden (solid triangles) and tar pit (open triangle) sites discussed in text. Mojave and Sonoran deserts stippled after Brown and Lowe (1978) and Küchler (1977).

the internal drainage basins of the western Mojave Desert from the Kern River drainage and the San Joaquin Valley. Robber's Roost is a series of rhyolitic plugs at 1190–1230 m elevation on the southeastern edge of the Scodie Mountains (35°35'45"N, 117°57'W), 4.3 km ene. of Freeman Junction. The packrat midden rockshelters are at ca. 1215 m.

The rainshadows of the Scodie Mountains, the Sierra Nevada, and the Transverse Ranges to the south are responsible for the general aridity of the interior Mojave and Great Basin deserts. The climatological means for Inyokern at 590 m, 14 km ne. of Robber's Roost, are 5.8°C for January, 29.2°C for July, and 106 mm/yr precipitation with 7.5% in the summer (June–August; NOAA 1986). Estimates of lapse rates for these climatic variables vary considerably. Major (1977) reported temperature lapse rates of $-0.45^{\circ}\text{C}/100\text{ m}$ for January means and $-0.60^{\circ}\text{C}/100\text{ m}$ for July means for Owens Valley north of Inyokern. Rowlands (1978) estimated -0.5°C to $-0.6^{\circ}\text{C}/100\text{ m}$ for January means in the northern Mojave Desert in general. A lapse rate of 9.4 mm/100 for annual precipitation was found for the western Mojave Desert in general (Rowlands 1978), for Death Valley from 1220 to 1830 m, and for the Kern River Canyon in the southwestern Sierra Nevada (Major 1977). Using these lapse rates the estimated climatic means for Robber's Roost at 1215 m are 2.5°C for January, 25.3°C for July, and 168 mm/yr precipitation with ca. 8% in the summer. If these lapse rates apply to the gradient above Robber's Roost, Skinner Peak at 2170 m would have -2.1°C January mean, 19.7°C July mean, and 255 mm/yr precipitation.

Three vegetation zones occur from 1000 to 2100 m on the east slope of the Scodie Mountains above Robber's Roost (Fig. 2, Table 1). Above 1900 m, all slopes support a mixed woodland of *Pinus monophylla*, *P. sabiniana*, *Quercus chrysolepis*, and occasional *Yucca brevifolia*. Important shrubs include *Artemisia tridentata*, *Eriogonum fasciculatum*, and *Purshia glandulosa*. An open woodland dominated by *Pinus monophylla* and *P. sabiniana* extends down to 1700 m on north slopes in Cow Heaven Canyon.

A mixed desertscrub with low shrubs grows from 1600 to 1900 m on hot, rocky east-facing slopes. Between 1300 and 1600 m a sparse desertscrub includes low shrubs of *Ericameria cooperi*, *E. cuneata*, *Purshia glandulosa*, and *Eriastrum densifolium* subsp. *mohavense*. On alluvial fans at these elevations a *Yucca brevifolia* desertscrub community with associated bunchgrasses (e.g., *Elymus elymoides*, *Oryzopsis hymenoides*, and *Stipa speciosa*) and shrubs (e.g., *Ephedra californica*, *Ericameria arborescens*, *Hymenoclea salsola*, and *Salvia dorrii*) is well developed.

Below 1300 m is a desertscrub dominated by *Larrea divaricata* and *Ambrosia dumosa* associated with other desert shrubs and bunchgrasses (Table 1). The Robber's Roost packrat midden site at

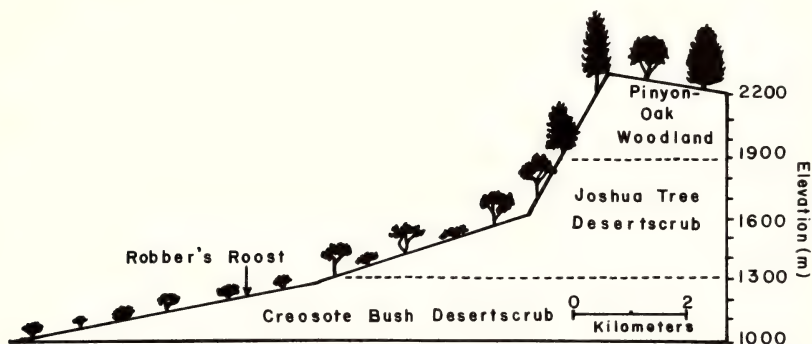


FIG. 2. Generalized vegetation zonation along an east-west transect above Robber's Roost (1215 m elev.) in the Scodie Mountains, Kern Co., California. Scale approximate.

1215 m is in this community (Fig. 3). *Ceratoides lanata*, *Encelia virginensis*, *Hymenoclea salsola*, *Salazaria mexicana*, and *Sphaeralcea ambigua* are scattered in the area. *Chrysothamnus nauseosus*, *Ericameria arborescens*, and *Ephedra californica* are restricted to relatively mesic microhabitats in the rhyolitic outcrops and along shallow washes. A small (ca. 1 m) plant of *Yucca brevifolia* was found at the edge of a small wash within 50 m of the midden rockshelter.

METHODS AND RESULTS

Packrat middens are hard, dark organic deposits that can be preserved in dry rockshelters for thousands of years. Middens are readily disaggregated by soaking in water, screened through soil sieves, oven dried, and hand sorted. The plant remains provide excellent samples of the local floras on rocky slopes and are excellent for radiocarbon dating. They contain well preserved plant remains collected within ca. 30 m that can often be identified to species.

Three packrat midden samples from Robber's Roost yielded a total of 22 plant taxa with 9–21 per sample. The specimens were identified by comparison with reference collections in the Laboratory for Paleoenvironmental Studies at the University of Arizona (Table 2). This number of taxa is adequate to describe the Late Wisconsin plant community at the site considering that 14–22 species were observed in modern Scodie Mountains communities (Table 1). Relative abundance classes in the fossil assemblages and modern communities were assigned from the most common (abundant = 5) to single specimens (rare = 1). Ranks of the intermediate classes (very common to uncommon, 4–2) varied depending on the total number of specimens identified. Plant nomenclature mostly follows Munz (1974); authorities for exceptions are included in Tables 1 and 2.

TABLE 1. PLANTS OBSERVED IN THE SCODIE MOUNTAINS, KERN CO., AND CUSHENBERRY CANYON, SAN BERNARDINO CO., CALIFORNIA. Authorities cited for names differing from Munz (1974). Relative abundance: 1 = rare, 2 = uncommon, 3 = common, 4 = very common, 5 = abundant. * = identified in Robber's Roost packrat middens.

Species	Scodie Mountains			Cushen- berry Canyon (1585- 1830 m)
	<1300 m	1300-1600 m	>1600 m	
<i>Ambrosia dumosa</i>	4	—	—	—
* <i>Artemisia tridentata</i>	—	—	3	5
<i>Atriplex canescens</i>	—	—	—	1
* <i>Ceanothus greggii</i>	—	—	3	2
<i>Ceratoides lanata</i> (Pursh)				
J. T. Howell	5	—	—	—
<i>Chrysothamnus nauseosus</i>	—	—	—	2
<i>Echinocereus engelmannii</i>	—	—	—	2
<i>Elymus elymoides</i> (Raf.) Swezey	1	4	—	—
<i>Encelia virginensis</i>	3	2	—	1
<i>Ephedra californica</i>	1	4	3	—
<i>Ephedra viridis</i>	—	—	—	3
<i>Ericameria cooperi</i> (A. Gray) Hall	—	1	—	2
* <i>Ericameria cuneata</i> (A. Gray)				
McClat.	—	2	—	—
<i>Ericameria laricifolia</i> (DC.)				
Urbatsch & Wussow	2	2	—	2
<i>Ericameria linearifolia</i> (T. & G.)				
Urbatsch & Wussow	—	—	—	2
<i>Eriodictyon crassifolium</i>	—	—	—	2
* <i>Eriogonum fasciculatum</i>	3	4	1	2
<i>Fremontodendron californicum</i>	—	—	—	2
<i>Gutierrezia microcephala</i>	—	—	—	2
<i>Hymenoclea salsola</i>	4	3	1	—
* <i>Juniperus californica</i>	—	—	2	—
<i>Juniperus osteosperma</i>	—	—	—	3
<i>Larrea divaricata</i> Cov.	3	—	—	—
* <i>Lepidium fremontii</i>	3	2	—	2
* <i>Lupinus excubitus</i>	—	3	—	—
<i>Lycium andersonii</i>	—	2	—	2
<i>Machaeranthera tortifolia</i>	2	3	—	—
<i>Mirabilis bigelovii</i>	4	3	—	2
* <i>Opuntia basilaris</i>	2	3	2	2
* <i>Opuntia echinocarpa</i>	3	2	—	2
<i>Opuntia phaeacantha</i>	—	—	—	2
<i>Oryzopsis hymenoides</i>	1	4	—	—
* <i>Penstemon incertus</i>	—	3	—	—
* <i>Pinus monophylla</i>	—	—	5	5
<i>Pinus sabiniana</i>	—	—	5	—
<i>Poa secunda</i> Presl.	—	—	—	2
<i>Prunus andersonii</i>	—	—	2	—
<i>Prunus fasciculata</i>	—	—	—	1
* <i>Purshia glandulosa</i>	—	—	3	2

TABLE 1. CONTINUED.

Species	Scodie Mountains			Cushen- berry Canyon (1585- 1830 m)
	<1300 m	1300-1600 m	>1600 m	
<i>Quercus chrysolepis</i>	—	—	4	—
* <i>Quercus turbinella</i>	—	—	—	2
<i>Salazaria mexicana</i>	3	3	—	2
<i>Salvia dorrii</i>	—	—	3	1
<i>Sphaeralcea</i> sp.	4	1	—	1
<i>Stipa speciosa</i>	3	5	—	2
<i>Tetradymia spinosa</i>	—	3	—	—
* <i>Yucca brevifolia</i>	1	4	1	3
Total =	19	22	14	31

Radiocarbon dates on twigs and seeds of *Juniperus californica* from the samples yielded ages of $12,870 \pm 400$ (A-1762, RR#1D), $12,960 \pm 270$ (A-1761, RR#2A), and $13,330 \pm 360$ (A-1763, RR#1C) yr B.P. (radiocarbon years before 1950). Attempts were not made



FIG. 3. View of packrat midden site at Robber's Roost, Kern Co., California. A pinyon-juniper woodland grew in the area from 12,870 to 13,330 yr B.P. in the Late Wisconsin.

to expand the three Late Wisconsin samples into a local chronology because of the rarity of fossil middens in the area.

Although the *Neotoma* teeth from the samples were not identifiable to species, they had rounded lophs characteristic of *N. albigula*, *N. fuscipes*, and *N. lepida* rather than the prismatic teeth of *N. cinerea* or *N. mexicana*. *Neotoma albigula* inhabits various communities in summer rainfall areas from southeasternmost California east to central Texas and the Mexican Plateau; it was probably not the builder of the Robber's Roost middens. More likely candidates are *N. lepida* of the Mojave Desert and nearby woodlands, or *N. fuscipes* of Sierran and coastal chaparral.

DISCUSSION AND CONCLUSIONS

The plant assemblages from the Robber's Roost packrat middens record a Late Wisconsin pinyon-juniper woodland dominated by *Juniperus californica* and *Pinus monophylla* in association with *Ceanothus greggii*, *Purshia glandulosa*, *Artemisia tridentata*, *Eriogonum fasciculatum*, *Yucca brevifolia*, *Quercus turbinella*, and *Ericameria cuneata* (Table 2). Twelve species (54.5%) identified from the samples no longer occur in the Robber's Roost area. Preliminary electrophoretic studies of phenolics including flavonoids suggest that the fossil junipers represent *J. californica* rather than *J. osteosperma*. The modern woodland above 1900 m is not a good analog of the Robber's Roost paleowoodland because *J. californica*, *C. greggii*, and *Q. turbinella* are rare or absent and *P. sabiniana* and *Q. chrysolepis* are associated with *P. monophylla*. The nearest populations of *J. californica* and *C. greggii* are 9 km nw. of Robber's Roost in Walker Pass at 1750 m elevation. Farther west, the vegetation begins a gradual transition to chaparral in South Fork Valley north of the Piute Mountains. The nearest populations of *Quercus turbinella* are in Kern Co. at Erskine Canyon in the northwestern Piute Mountains (ca. 40 km w.) and in the northeastern Tehachapi Mountains (47 km ssw.; Twisselman 1967; Fig. 1).

Estimates of climatic parameters for Robber's Roost in the Late Wisconsin using lapse rates discussed above for a 685 m minimum lowering of *Pinus monophylla* in the Scodie Mountains are -0.75°C mean for January, 21.3°C for July, and 218 mm/yr precipitation with little in summer. As mentioned above the Scodie Mountains woodland is a poor analog, suggesting the modern climates may also be different. Different lapse rates in the Late Wisconsin would yield different estimates. The paleoclimatic estimates are within the climatic limits estimated for modern pinyon-juniper woodlands in the mountains of the eastern Mojave Desert by Thorne et al. (1981): e.g., January mean less than 4°C , July mean less than 25.5°C , and annual precipitation greater than 250 mm/yr with 165–185 mm in

TABLE 2. PLANT MACROFOSSILS IDENTIFIED FROM PACKRAT MIDDENS FROM ROBBER'S ROOST, SCODIE MOUNTAINS, KERN CO., CALIFORNIA. Authorities cited for names differing from Munz (1974). Relative abundance: 1 = rare, 2 = uncommon, 3 = common, 4 = very common, 5 = abundant. Distribution: n = presently occurs in Robber's Roost; e = extralocal, no longer lives in area; ka = thousands of years ago.

Species	Material	RR#1D (12.9 ka)	RR#2A (13.0 ka)	RR#1C (13.3 ka)
<i>Ambrosia</i> sp.	burs	—	1n	1n
<i>Amsinckia tessellata</i>	nutlets	—	1n	—
<i>Artemisia tridentata</i>	leaves, wood	—	2e	3e
<i>Ceanothus greggii</i>	leaves	2e	3e	4e
<i>Chrysothamnus</i> sp.	achenes, involucre	—	1n	1n
<i>Encelia</i> sp.	achenes	—	1n	—
<i>Ephedra</i> sp.	stems	—	1n	—
<i>Eriastrum</i> sp.	leaves	—	1e	—
<i>Ericameria arborescens</i> Greene	involucre, leaves	—	1n	1n
<i>Ericameria cuneata</i> (A. Gray) McClat.	leaves	1n	2e	—
<i>Eriogonum fasciculatum</i>	inflorescence, leaves, stem	—	1n	1n
<i>Juniperus californica</i>	seeds, stems	5e	5e	5e
<i>Lepidium fremontii</i>	capsules	—	1n	1n
<i>Lupinus excubitus</i>	leaves	2e	2e	3e
<i>Lycium</i> sp.	leaves	2e	2e	2e
<i>Opuntia basilaris</i>	seeds	—	2n	—
<i>Opuntia echinocarpa</i>	spines	2n	2n	2n
<i>Pensilemon incertus</i>	seeds, fruit, leaves, stems	—	—	2e
<i>Pinus monophylla</i>	seeds, cone scales, leaves	3e	2e	2e
<i>Purshia glandulosa</i>	fruit, leaves	1e	3e	3e
<i>Quercus turbinella</i>	leaves	—	1e	—
<i>Yucca brevifolia</i>	leaves	2e	2e	—
Total = 22		9	21	14

the cool seasons (September to May). This would represent an increase in annual and winter precipitation at Robber's Roost of about 36%.

An excellent modern analog to the Robber's Roost paleocommunity is on the north slopes of the San Bernardino Mountains above the Lucerne Valley (Fig. 1) in San Bernardino Co. An extensive pinyon-juniper woodland in Cushenberry Canyon (1830 m) is dominated by *Pinus monophylla*, *Juniperus osteosperma*, and *Yucca brevifolia* and also includes *Atriplex canescens*, *Artemisia tridentata*, *Ceanothus greggii*, *Chrysothamnus nauseosus*, *Ephedra viridis*, *Ericameria linearifolia*, *Eriogonum fasciculatum*, *Opuntia basilaris*, *O. echinocarpa*, *O. phaeacantha*, *Purshia glandulosa*, *Quercus turbinella*, and *Salvia dorrii*. *Encelia virginensis* and *Lepidium fremontii* were seen just below at 1585 m. *Juniperus californica* is present in the lower portion of the woodland. This area is 500–700 m higher than Robber's Roost and 170 km to the southeast. Similar woodlands can be found in other areas along the desert slopes of the San Bernardino and San Gabriel mountains.

The Robber's Roost paleowoodland is also similar to modern woodlands isolated in the mountains of the eastern Mojave Desert (Thorne et al. 1981). Late Wisconsin pinyon-juniper woodlands with *Pinus monophylla* have been recorded in the Mojave Desert from Ord Mountain (King 1976), the Turtle Mountains (Wells and Berger 1967), and Clark Mountain (Mehring and Ferguson 1969) in California and the Newberry Mountains (Leskinen 1975), Spring Range (Van Devender and Spaulding 1979), Sheep Range (Spaulding 1981), and Specter Range (Spaulding 1985) in Nevada. Xeric woodland assemblages dominated by *Juniperus californica* with low levels of *Pinus monophylla*, *Yucca brevifolia*, and *Y. whipplei* have been found as low as 510 m in the Whipple Mountains just above the Colorado River in eastern San Bernardino Co. (Van Devender and Spaulding 1979, Van Devender et al. 1987). These relict distributions of modern woodlands and their fossil records suggest that pinyon-juniper woodland was widespread across the central and southern Mojave Desert in the Late Wisconsin (Wells 1986, Betancourt 1986).

Full-glacial packrat midden records from King's Canyon in the Sierra Nevada (170 km nnw. of Robber's Roost) record the expansion of *Pinus monophylla* even farther to the west (Cole 1983). Fossils of *P. monophylla* and *J. californica* (including *J. osteosperma*) were reported from the Late Pleistocene McKittrick asphalt deposits at 320 m elevation in the San Joaquin Valley 170 km wsw. of Robber's Roost (Mason 1944). The plant fossils were associated with extinct mammals characteristic of the Rancholabrean Land Mammal Age including *Bison*, *Camelops*, *Equus*, *Hemiauchenia*, *Mammuthus*, and *Mammuthus* (Harris 1985). A middle Wisconsin radiocarbon age ($38,000 \pm 2500$ yr B.P.) was obtained on plant materials

from the site (Kurtén and Anderson 1980). These records suggest that many of the disjunct populations of Great Basin plants did not disperse into the Sierra Nevada during the "warm, dry Xerothermic" dispersal (=middle Holocene; Taylor 1976, Axelrod 1981) but in glacial climates in the Wisconsin if not earlier.

The Robber's Roost paleoflora is especially interesting because of its location near the eastern base of the Sierra Nevada. A number of trees that potentially could have dispersed southward along the main axis or eastward from the mesic west slopes of the Sierra or northwest from the Transverse Ranges were not found; e.g., *Abies concolor*, *A. magnifica*, *Calocedrus decurrens*, *Juniperus occidentalis*, *Pinus coulteri*, *P. lambertiana*, *P. jeffreyi*, *P. ponderosa*, *Pseudotsuga macrocarpa*, *Quercus agrifolia*, *Q. douglasii*, *Q. lobata*, or *Sequoiadendron giganteum*. Thompson et al. (1985) reported an eastward expansion of *J. occidentalis* from the Sierra Nevada into the Winnemucca Lake Basin of Nevada in the Great Basin. Plants indicative of the *Adenostoma fasciculatum*-dominated chaparral of the Los Angeles Basin have not been found in middens.

Packrat middens from the Mojave and Sonoran deserts have yielded records of some plants now found in the chaparral and woodlands of the interior slopes of the mountains of southern California with more extensive eastern distributions in the Late Wisconsin and early Holocene. Most of them presently have disjunct populations in woodland, chaparral, or desertscrub communities in Arizona or Sonora (e.g., *Artostaphylos pungens*, *Ceanothus greggii*, *Eriogonum fasciculatum*, *Juniperus californica*, *Nolina bigelovii*, *Quercus chrysolepis*, *Q. dunni*, *Q. turbinella*, *Yucca brevifolia*, and *Y. whipplei*). Most Late Wisconsin dispersals of woodland, chaparral, or desertscrub species into the Mojave Desert recorded by packrat midden fossils were from the north or northeast.

Plant remains in packrat middens from Robber's Roost and other areas in the Mojave Desert provide insight into the historical components in modern communities. The modern vegetation of Robber's Roost is a mixture of species that were present in the Late Wisconsin woodland and warm desert species that dispersed into the area in the Holocene. The regional vegetation of the western Mojave Desert reflects similar historical processes with pinyon-juniper woodlands contracted to isolated mountaintops or the lower elevational zones of larger mountain ranges. In the Late Wisconsin a Mojave desertscrub with *Larrea divaricata* and *Yucca brevifolia* was present below 310 m in the Picacho Peak area in Imperial Co., California (Van Devender et al. 1985, Cole 1986). The area is just north of Yuma in the modern Lower Colorado River Valley subdivision of the Sonoran Desert. The *Larrea divaricata*-*Ambrosia dumosa* desertscrub of much of the Mojave Desert developed in the last 11,000 years as these species and their associates migrated from

their glacial refugium in the Lower Colorado River Valley and the Gran Desierto surrounding the head of the Gulf of California in Sonora and Baja California. Great Basin elements of the paleo-woodlands survive today in the region as elevational zones dominated by *Artemisia tridentata* and in mixed desertscrub communities in the western Mojave Desert (e.g., *Artemisia spinescens*, *Atriplex confertifolia*, and *Ceratoides lanata*).

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ANNOUNCEMENT

NEW PUBLICATION

BARBOUR, M. G. and W. D. BILLINGS, eds. 1988. *North American terrestrial vegetation*. Cambridge Univ. Press, New York. 434 pp. ISBN 0-521-26198-8 (clothbound), \$49.50. [Vegetation of North America including tropical areas. Thirteen chapters, each separately authored and with its own references. Illustrated with black and white photographs, maps, and diagrams.]

THE ABUNDANCE OF PLANTS BEARING EXTRAFLORAL NECTARIES IN COLORADO AND MOJAVE DESERT COMMUNITIES OF SOUTHERN CALIFORNIA

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ABSTRACT

Measurements of the cover and frequency of EFN-bearing plants in seven warm desert communities in California revealed some of the highest levels of abundance of EFN-bearing plants that have been recorded for the temperate zone. The desert wash communities of both deserts had the highest covers (28 and 24%) and frequencies (0.27, 0.27) of EFN-bearing plants, whereas the sand dune communities had the lowest levels of abundance of EFN-bearing plants with covers of 2 and 0.0% and frequencies of 0.01 and 0.0. Colorado Desert communities had higher covers, frequencies, and numbers of EFN-bearing plants than Mojave Desert communities. The EFN antiherbivore defense system is predicted to be also common in other warm-dry communities of the world because those environments have an abundance of ants and plant groups, such as mimosoid legumes and cacti, known to have many EFN-bearing species. The EFN defense system may be particularly well suited to plants growing in warm-dry zones.

Extrafloral nectaries are nectar-secreting glands occurring most commonly on the vegetative parts of plants, but also at other sites such as developing fruit and the external parts of flowers. Instead of attracting pollinators, extrafloral nectaries (EFN's) have been shown to promote mutualistic interactions between plants and the insects, especially ants, that visit the EFN's. The insect participants gain sugars, amino acids, and water from the EFN's and benefit the plants by reducing the damage caused by the plant's herbivores (Janzen 1966, Bentley 1977a, Tilman 1978, Pickett and Clark 1979, Keeler 1980, Schemske 1980). At least 73 angiosperm families with almost 1000 species, and a few ferns have EFN's (Keeler 1979b). Plants with EFN's occur in most parts of the world (Zimmermann 1932, Schnell et al. 1963) and appear to be most common in the tropics (Bentley 1977b).

The abundance of EFN plants in plant communities has been examined in Costa Rica (Bentley 1976), Jamaica (Keeler 1979a), Nebraska (Keeler 1979b), Northern California (Keeler 1981a), Arizona (Keeler 1981b), and Hawaii (Keeler 1985). The cover of EFN plants has been found to be highest in the communities in Costa Rica (40–80%) and in the aspen (*Populus tremuloides* Michx.) dom-

inated mountain forests of Arizona (39%). The lowest covers of EFN plants were in the Nebraska communities (0.0–8%) and in northern California where no EFN plants were found in the four communities sampled.

Zimmermann (1932) thought that xerophytes, as a rule, lacked EFN's and for this reason believed the dry floras of California to have practically no EFN plants. Except for *Helianthella californica* Gray (Keeler 1981a), no native EFN plants have been reported from California (Buckley 1982). After observing EFN's on cacti growing in California's deserts, I suspected that plants with EFN's were more abundant in California than was previously known. A greater abundance of plants with EFN's in California's deserts was also suggested by the abundance of ants (Wheeler and Wheeler 1973), which has been correlated with the abundance of EFN plants in other communities (Bentley 1976). The object of this study was to learn how abundant EFN plants might be in some California desert communities.

METHODS

The abundance of EFN plants was determined by measuring their frequency and cover in four Colorado Desert and three Mojave Desert communities in southern California during March 1986. Frequency was determined by scoring the presence or absence of EFN plants at 1 m intervals along three 100 m transects through each community. Cover was determined by measuring to the nearest cm the linear distance occupied by EFN plants along each of the transects. Detection of EFN plants was made by direct observation of secreting EFN's on the plants, which was often aided by the presence of ants and other insects tending the nectaries. Locating EFN plants was made easier by examining species (and their relatives) previously reported to bear EFN's. The percentages of the floras with EFN plants in the areas studied was made by identifying the species, known to me, to have EFN in "Plants of Deep Canyon" (Zabriskie 1980), the area of the Colorado Desert transects, and in "A Flora of the Higher Ranges and Kelso Dunes of the Eastern Mojave Desert in California" (Thorne et al. 1981), the area of the Mojave Desert transects.

Colorado Desert Transects

The Colorado Desert transects were taken at the Phillip L. Boyd Deep Canyon Desert Research Center of the University of California. This area lies on the northeast slopes of the Santa Rosa Mountains and the adjacent southwest slopes of Coachella Valley, Riverside Co., California between 116°–117°W and 33°–34°N. The

Colorado Desert is the northwestern subsection of the Sonoran Desert, and is lower in altitude and more arboreal in character than the Mojave. Creosote bush scrub occupies the largest areas in both the Colorado and Mojave deserts (Munz and Keck 1959).

1. Creosote bush scrub—on rocky alluvial fan, west of the Channel of Deep Canyon Creek, 300 m elev. Common plants: *Encelia farinosa* A. Gray (Compositae), *Fouquieria splendens* Engelm. (Fouquieriaceae), *Larrea divaricata* Cav. (Zygophyllaceae), and *Opuntia* spp. (Cactaceae).

2. Desert wash—sand and pebbles, Deep Canyon creek wash, 265 m elev. Common plants: *Acacia greggii* A. Gray and *Cercidium floridum* Benth. (Leguminosae), *Chilopsis linearis* (Cav.) Sweet (Bignoniaceae), and *Hyptis emoryi* Torr. (Labiatae).

3. *Yucca*-galleta grass—sand and rock hillside, adjacent to Hwy. 74 overlooking Deep Canyon, 820 m elev. Common plants: *Agave deserti* Engelm. and *Yucca schidigera* Roez. ex Ortgies (Agavaceae), *Fouquieria splendens* and *Hilaria rigida* (Thurb.) Benth. ex Scribn. (Gramineae).

4. Sand dunes—Coachella Valley floor east of Thousand Palms, 40 m elev. Common plants: *Atriplex* spp. and *Salsola australis* R. Br. (Chenopodiaceae), *Larrea divaricata* and *Prosopis juliflora* (Sw.) DC. (Leguminosae).

Mojave Desert Transects

The Mojave Desert transects were located on the northern side of the Granite Mountains and at Kelso Dunes in San Bernardino Co., California at approximately 116°W and 35°N. The Mojave Desert is intermediate between the cold-temperate Great Basin Desert and the subtropical Colorado Desert (Turner 1982) and has a lower diversity of perennial plants than the Colorado Desert (Vasek and Barbour 1977). The average annual rainfall for the Mojave study areas is less than 200 mm (estimated from Thorne et al. 1981) and 90–150 mm for the Colorado Desert sites (estimated from I. P. Tinginan, unpublished booklet, "Natural History of Deep Canyon"). The average annual temperature for the Mojave sites is estimated to be around 26°C (Thorne et al. 1981) and higher for Deep Canyon, where it rarely freezes.

5. Sand dunes—eastern slope of Kelso Dunes, 900–1000 m elev. Common plants: *Astragalus* sp. (Leguminosae), *Croton californicus* Muell. Arg. (Euphorbiaceae), and various grasses.

6. Creosote bush scrub—sand and rock, alluvial fan, northern slope of the Granite Mts., 1250 m elev. Common plants: *Coleogyne ramosissima* Torr. (Rosaceae), *Eriogonum* spp. (Polygonaceae), *Larrea divaricata* and *Salazaria mexicana* Torr. (Labiatae), and *Yucca schidigera*.

7. Desert wash—boulders and sand, northern slope of Granite

Mts., 1350 m elev. Common plants: *Acacia greggii*, *Ephedra* sp. (Ephedraceae), *Isomeris arborea* Nutt. (Capparidaceae), *Prunus fasciculata* (Torr.) Gray (Rosaceae), and *Rhus trilobata* Nutt. ex T. & G. (Anacardiaceae).

RESULTS

The plants observed to bear EFN's are listed in Table 1. All 11 species had active secreting EFN's in either the Colorado or Mojave Desert study areas, or both. The largest number of the species found to possess EFN's were cacti. The four *Opuntia* species had EFN's located on the areoles of the newly formed pads, flower buds, and flowers. The EFN's of *Ferocactus* were tubercles located above the areoles on the inside of the ring of flowers on top of the cacti. The EFN's of all cacti, except *O. acanthocarpa* Engelm. and Bigel., were tended by ants. The EFN's of *Chilopsis* were located on the leaf blades and were variable in their occurrence both within and between trees. The EFN's of ocotillo (*Fouquieria splendens*) were located on the flower buds, where relatively large 5 mm diameter drops of sweet tasting viscous nectar accumulated. *Acacia greggii* had small EFN's located on the leaves along the primary rachis between the branching secondary rachis bearing the leaflets. *Prosopis juliflora* bore EFN's on the rachis between the leaflets and also on the leaf petioles. Ants were tending its EFN's. The *Prunus* species had EFN's at the bases of their leaf blades. *Prunus fasciculata* had large numbers of small parasitic wasps (mainly Chalcidoidea) visiting its EFN's. In addition to the hymenoptera (ants and wasps) visiting the EFN's, lady beetles (*Hippodamia convergens* Guerin-Meneville) were observed on the EFN's of *Opuntia echinocarpa* Engelm. & Bigel. and small unidentified flies were observed feeding on the nectaries of *Chilopsis*.

The abundance of EFN plants in the different communities of the Colorado and Mojave deserts is shown in Table 2. The desert wash communities of both deserts had the highest covers (27.74%, 23.89%) and frequencies (0.277, 0.266) of EFN plants. The sand dune communities, with 1.36% and 0.0% covers, and 0.016 and 0.0 frequencies, had the lowest abundance of species with EFN's. The creosote bush scrub communities were intermediate in both deserts (cover 6.58%, 0.07%; frequency 0.120, 0.003). The communities of the Colorado Desert had, on average, a higher EFN plant cover (\bar{x} = 9.8%) and frequency (\bar{x} = 0.118) than those of the Mojave cover (\bar{x} = 8.0%) and frequency (\bar{x} = 0.090). The \bar{x} number of EFN plant species was also higher in the Colorado communities with 3 vs. 1.66 species for the Mojave communities.

The percentages of species with EFN's in the native flora were 0.95% (1/105) for Kelso Dunes and 2.61% (10/382) for the Granite Mountains of the Mojave, and 3.20% (18/562) for Deep Canyon of the Colorado.

TABLE 1. PLANTS OBSERVED TO HAVE EXTRAFLORAL NECTARIES (EFN) AT THE COLORADO AND MOJAVE DESERT STUDY SITES. C = Colorado, M = Mojave. *Previously unreported EFN plant. †All species were observed to secrete nectar. ‡EFN's were observed on flower buds and bracts in May 1987, in southern Nevada and were visited by lady beetles.

Species	Desert	EFN site	Remarks ¹
Cactaceae			
<i>Opuntia acanthocarpa</i> Engelm. & Bigel.	C, M	areoles	Pickett and Clark 1979
* <i>O. basilaris</i> Engelm. & Bigel.	C, M	areoles	ants tending
* <i>O. bigelovii</i> Engelm.	C	areoles	ants tending
* <i>O. echinocarpa</i> Engelm. & Bigel.	C, M	areoles	lady beetles and ants tending
<i>Ferocactus acanthodes</i> (Lem.) Britt. & Rose	C	above areoles	ants tending
Bignoniaceae			
* <i>Chilopsis linearis</i> (Cav.) Sweet	C	leaf blade ²	a few flies taking nectar
Fouquieriaceae			
* <i>Fouquieria splendens</i> Engelm.	C	flower buds	
Leguminosae			
* <i>Acacia greggii</i> Gray	C, M	leaf rachis	ants tending
<i>Prosopis juliflora</i> (Sw.) DC.	C	leaf rachis and petiole	
Rosaceae			
* <i>Prunus fasciculata</i> (Torr.) Gray	M	leaf blade	misc. parasitic wasps foraging
* <i>Prunus fremontii</i> Wats.	C	leaf blade	

TABLE 2. ABUNDANCE OF PLANTS WITH EXTRAFLORAL NECTARIES IN THE COLORADO AND MOJAVE DESERTS. Combined data for three 100 meter transects per community.

Community location	Frequency n/300 points	% cover n/300 meters	Number of EFN species
Colorado Desert			
1. Creosote bush scrub	0.120	6.58	6
Deep Canyon	36/300	19.7/300	
2. Desert wash	0.277	27.74	2
Deep Canyon	83/300	83.2/300	
3. Yucca agave galeata grass	0.060	3.65	3
Deep Canyon	18/300	10.9/300	
4. Sand dunes	0.016	1.36	1
Cocachella Valley	5/300	4.1/300	
Mojave Desert			
5. Sand dunes	0.000	0.00	0
Kelso	0/300	0/300	
6. Creosote bush scrub	0.003	0.07	1
Granite Mt.	1/300	0.2/300	
7. Desert wash	0.266	23.89	4
Granite Mts.	80/300	71.7/300	

DISCUSSION

The detection of cacti previously unreported to bear EFN was predicted by their occurrence in other cacti (Lloyd 1908, Pickett and Clark 1979). Similarly, many *Prunus* (Dorsey and Weiss 1920) and *Acacia* species (Delpino 1886) are known to bear EFN's. *Chilopsis* was suspected to have EFN's because most members of the Bigoniaceae have them (Elias 1983). Less expected were the EFN's in ocotillo (*Fouquieria splendens*) since few members of the Fouquieriaceae have them (Elias 1983).

Although the abundance of EFN plants in some of the desert communities of this study was quite high (24 and 28% cover), none approached the high levels (40–80%) measured in three dry tropical forest habitats in Costa Rica (Bentley 1976). More similar were the Jamaican lowland (Keeler 1979a) and Hawaiian *Acacia koa* Grey (Keeler 1985) communities with covers by EFN plants of 28 and 21%. Most temperate communities that have been measured have much lower abundances of EFN plants than found in this study. The exceptions are Arizona aspen forest (39%) and an Arizona Sonoran Desert community, found to have a cover of 22% (Keeler 1981b). The cover for that Arizona desert community is similar to the cover (24 and 28%) of desert washes measured in this study.

The only published accounts of the frequency of EFN species in floras are for Hawaii and Nebraska. Keeler (1979b, 1985) found 2.5% of the indigenous species in Nebraska to have EFN's and 1.5% of Hawaiian natives in Hawaii Volcano National Park to bear EFN's.

The figures for this study (0.95, 2.61, and 3.20%) are similar and noteworthy because most of the desert community EFN plant covers are much greater than in Nebraska and most of the Hawaiian communities sampled. These differences are explained by the presence of EFN's in species that are both abundant and of large stature, such as *Chilopsis*, *Acacia*, *Prosopis*, *Fouquieria*, and *Prunus*. High plant covers of EFN plants have been measured in other communities having few or single or large statured EFN plants, such as *Acacia koa* in Hawaii and *Populus tremuloides* in Arizona.

The desert plants in this study comprised some of the highest EFN plant covers that have been measured in the temperate zone communities. I predict that EFN plants are also common in many of the world's warm deserts and other hot dry biomes such as savanna and tropical scrub.

A number of the taxa found to bear EFN's in this study have dryland relatives that are known to bear EFN's. Delpino (1886) found that 172 of the 258 *Acacia* and 11 of the 15 *Prosopis* species he examined bore EFN's. Broughton (1981) found EFN's in all 42 species of Australian *Acacia* that she studied, including those from the interior desert areas which had formerly been thought to lack EFN's. EFN's also occur in *Acacia* species that are native to Central America (Janzen 1966), the Caribbean and South America (Keeler pers. comm.), Africa (Ross and Gordon-Gray 1966), and India (Bhattacharyya and Maheshwari 1971). EFN's are also common in species of other mimosoid genera such as *Mimosa*, *Albizia*, and *Leucaena* (Bhattacharyya and Maheshwari 1971) that are prominent members of the world's warm-dry floras. The prevalence of EFN's in species of cacti in the genera *Opuntia* and *Echinocactus* (Lloyd 1908), *Ferocactus* (Blom and Clark 1980, Ruffner and Clark 1986), and others native to both North America and South America, further support the probability of an abundance of EFN plants in the New World warm deserts and tropical scrub communities.

The general richness and abundance of ants in the world's desert and warm-dry communities also supports the prediction of high levels of abundance of EFN-bearing plants in those regions, as they did in the deserts of southern California.

The use of a water based antitherbivore defense system may appear to be an inappropriate strategy for arid land plants; however, growth and reproduction in warm desert plants usually occur only in periods of increased water availability. Since secretion in EFN's is most active in expanding foliage and reproductive structures (Bentley 1977b, and this study), EFN defense is used during periods of water availability. The greatest abundance of EFN-bearing plants in this study was desert washes, areas where plants have greater access to water.

Protection of new growth and reproductive tissues may be rela-

tively more important in desert plants, since the possibilities of regrowth of tissues lost to herbivores is restricted by limited water. The EFN defense may be particularly well suited to these arid land plants because the vulnerable tissues are protected as they are being produced. EFN defenses also have the advantage of being effective against both specialist and generalist insect herbivores, which is usually not the case for specific chemical defenses (Beattie 1985).

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ANNOUNCEMENT

PUBLICATION AVAILABLE

Biology of the California Islands—Proceedings of the First Symposium (R. W. Philbrick, ed.). 1967. 363 pp. Hard cover, \$3.75. [We have a large number of copies of the first Symposium in mint condition that we would like to get into the hands of interested persons.] Available from the Santa Barbara Botanic Garden, 1212 Mission Canyon Road, Santa Barbara, CA 93105. Price includes shipping and California sales tax.

GENERIC RELATIONSHIPS AND TAXONOMY OF *ACAMPTOPAPPUS* (COMPOSITAE: ASTEREAE)

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ABSTRACT

Acamptopappus comprises *A. sphaerocephalus* var. *sphaerocephalus* and var. *hirtellus*, and *A. shockleyi*, taxa of the southwestern deserts of the United States. Characteristics shared by these taxa include extremely long-villous achenes, a pappus of long, somewhat erose scales with lanceolate to spatulate apices, deeply alveolate receptacles, short, funnelform disk corollas with deep sinuses and reflexed lobes, very broad phyllaries with very broad, scarious margins, and nearly globose capitula. Chromosome numbers of all taxa are $n = 9$. The probable closest relatives of this outlying genus are to be found among larger genera of Astereae having $x = 9$, particularly the *Chrysothamnus*—*Ericameria*—*Macronema* alliance.

Acamptopappus (A. Gray) A. Gray comprises three taxa of the Mojave and Sonoran deserts of the southwestern United States (Figs. 1, 2). The taxa are distinctive in appearance, with very light green foliage, whitish stems, nearly globose capitula, phyllaries nearly as broad as long, and the most villous achenes of all North American Astereae. No treatment encompassing all three taxa has previously been published, except in floras. This paper circumscribes these taxa, and discusses the possible relationships of *Acamptopappus* with other genera of Astereae.

TAXONOMIC HISTORY

Gray (1849) named sect. *Acamptopappus* of *Haplopappus* Cass. to accommodate *H. sphaerocephalus* Harvey & A. Gray in A. Gray (1849). It was based on a specimen collected by Thomas Coulter in 1832 that had been forwarded to Gray between 1846 and 1848 by W. H. Harvey, Coulter's successor as curator of the herbarium of Trinity College, Dublin (Coville 1895). Later, Gray (1873) accorded generic status to *Acamptopappus*, a move with which Hall (1928, p. 365) concurred. In 1882, Gray described *A. shockleyi*. Jones (1898) established *A. microcephalus*, which was placed in synonymy with *Ericameria cooperi* (A. Gray) H. M. Hall by Blake (1929), when he named *A. sphaerocephalus* var. *hirtellus*. No additions have been made to the genus as a result of the present study, although questions about the types are clarified in comments following the descriptions of taxa.

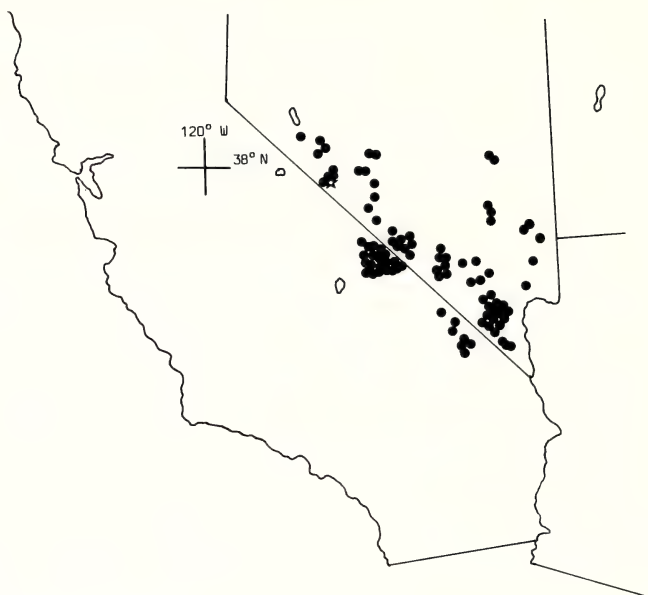


FIG. 1. Distribution of *Acamptopappus shockleyi*. Each symbol may represent one or more collections. Type locality indicated by star.

METHODS

Standard herbarium techniques were used to study 1182 specimens of the three taxa, including types, borrowed from or observed at ARIZ, ASU, CAS, COLO, F, GH, JEPS, K, LL, MO, NY, POM, RM, RSA, SD, TCD, TEX, UC, US, and UTC. For comparison of generic features, specimens of *Chrysothamnus*, *Eastwoodia*, *Ericameria*, *Petradoria*, *Stenotus*, and *Vancelevia* belonging to COLO, LL, RM, and TEX were studied. *Acamptopappus* taxa were observed in the field during trips taken in 1984 and 1986.

Achenes, style-branches, corollas and pappus members used for scanning electron microscopy were carefully removed from herbarium specimens (COLO, LL, RM, or TEX). Achenes and pappus were mounted on stubs with double-stick tape; style-branches and corollas were rehydrated by soaking in Wetter's solution (Wetter 1983), rinsed, and then mounted with double-stick tape. Stubs were sputter-coated with ca. 400 nm gold, and observed on an AMR 1000A at 20 kV.

DISCUSSION

Morphology. The two species of *Acamptopappus* are very similar to one another (Table 1, Fig. 3), except that *A. sphaerocephalus* plants

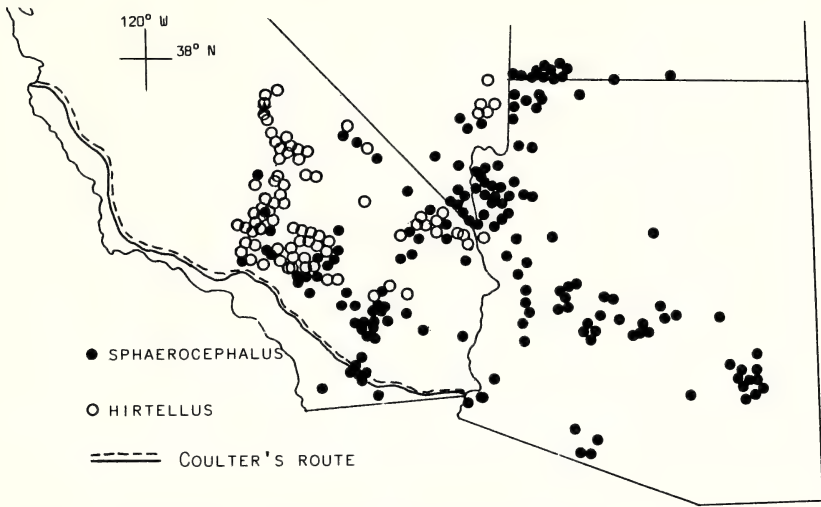


FIG. 2. Distribution of *Acamptopappus sphaerocephalus* var. *hirtellus* and var. *sphaerocephalus*. Each symbol may represent one or more collections. Type locality for var. *hirtellus* indicated by star. Route of Thomas Coulter (Coville 1895) indicated by double line; see comments under description of var. *sphaerocephalus* for explanation.

are usually slightly larger (to 4 dm) than those of *A. shockleyi* (to 3.3 dm), are more highly ramified, have narrower leaves, and have smaller, more numerous and occasionally clustered capitula that are eradiate and have fewer disk florets.

The pappus of *A. shockleyi* usually consists of 17–30 moderately erose, white scales. Ray floret pappus apices usually are lanceolate to acute, whereas those of the disk florets are more spatulate (Fig. 4a); the pappus elements of *A. sphaerocephalus* disk florets are spatulate.

Both species have narrowly triangular-lanceolate disk style-branch appendages that are acute and flattened on the adaxial face, and have collecting hairs that are of moderate length (Fig. 4a). Disk corolla epidermes (Fig. 5a) of the two species of *Acamptopappus* are identical. Ray-corolla epidermis of *A. shockleyi* is shown in Fig. 5b.

Achenes of *Acamptopappus* species are actually cylindric, but appear obconic in outline because they are covered with the longest and densest *zwillingshaares* that I have seen in any taxon of Astereae. Anderson and Weber (1974) noted that there are “long, isotropic, non-glandular (shag) hairs” present with the “anisotropic duplex hairs” on *Acamptopappus* achenes. However, I found that all trichomes are of the normal “anisotropic duplex” type exemplified by those of *Stenotus acaulis* (Fig. 5c), except that some are twisted and contorted (Fig. 5d). The latter are usually concealed by a layer of

TABLE 1. DISTINGUISHING MORPHOLOGICAL FEATURES OF *Acamptopappus* SPECIES, *Amphipappus*, *Eastwoodia*, AND *Vanceleva*. Adapted in part from Anderson and Weberg (1974).

	<i>Acamptopappus shockleyi</i>	<i>Acamptopappus sphaerocephalus</i>	<i>Amphipappus fremontii</i>	<i>Eastwoodia elegans</i>	<i>Vanceleva stylosa</i>
Leaves	Narrowly obovate, spreading-ascendant, uninervate, non-resinous	Mostly linear, spreading-ascendant, uninervate, non-resinous	Obovate or elliptic, spreading, uninervate, scarcely resin-dotted	Linear to lanceolate, ascendant, uninervate, glandular-punctate	Linear-lanceolate, spreading to falcate, trinervate, resinous
Capitulescence	Solitary (Fig. 3a)	Solitary or occasionally cymosely clustered (Fig. 3b)	Cymose clusters (Fig. 3c)	Solitary or open cymose panicle	Solitary to cymose
Capitulum shape	Hemispheric (Fig. 3a)	Hemispheric to nearly spheric (Fig. 3b)	Cylindric (Fig. 3c)	Broadly turbinate	Campanulate to campanulate with umbilicate base
Phyllaries	13-18(-23), 2-3 series, broad, flat, chartaceous; margins broad, scarious; apices rounded	11-18(-20), 2-3 series, broad, flat, chartaceous; margins broad, scarious; apices rounded	7-12, 2-3 series, broad, semi-plicate; margins broad, scarious; apices rounded	ca. 50, 4-5 series, narrow, flat to recurved; margins usually not scarious; apices acuminate	50-60, 4-5 series, narrow, often squarrose; margins usually not scarious; apices acute-acuminate
Receptacle	deeply alveolate, with projections between florets	deeply alveolate, with projections between florets	alveolate	alveolate, paleaceous	alveolate
Ray florets	5-14	0	1-2, barely exceeding involucre	0	0
Disk florets	30-80, hermaphroditic	(13-)14-24(-27), hermaphroditic	3-7, functionally staminate	ca. 30-40, hermaphroditic	(31-)35-45(-48), hermaphroditic

TABLE 1. CONTINUED.

	<i>Acamptopappus shockleyi</i>	<i>Acamptopappus sphaerocephalus</i>	<i>Amphipappus fremontii</i>	<i>Eastwoodia elegans</i>	<i>Vancevea stylosa</i>
Disk corollas	Broadly funnelform; sinuses deep; lobes spreading to re- flexed	Broadly funnelform; sinuses deep; lobes spreading to re- flexed	Broadly funnelform; sinuses deep; lobes reflexed to re- curved	Tubular-funnelform; sinuses shallow to deep; lobes laxly erect	Tubular-funnelform; sinuses shallow; lobes erect to re- flexed
Pappus	(15-)18-30(-38) flat, slightly erose scales, sometimes tortuous	(15-)17-26(-28) flat, slightly erose scales, sometimes tortuous	15-20 broad, flat, tortuous, deeply barbellate bristles	5-8 ascendant, awl- shaped, paleaceous awns	(12-)15-18 spreading, awl-shaped, thinly paleaceous awns
Achenes	Extremely densely long-villous; outer trichomes straight; inner ones tor- tuous	Extremely densely long-villous; outer trichomes straight; inner ones tor- tuous	Scantily long-villous; trichomes tortuous	Somewhat pubescent above	Nearly glabrous



FIG. 3. Line drawings of habits (left) and capitula (right): a. *Acamptopappus shockleyi* (Henrickson 9584, TEX); b. *A. sphaerocephalus* var. *sphaerocephalus* (M. E. Jones s.n., TEX); c. *Amphipappus fremontii* var. *fremontii* (Cronquist 10649, TEX). Scale bars = 2 cm.

straight trichomes, much as the downy underhairs of animal fur are covered by long, straight guard hairs. The adaptive significance of this arrangement is obscure, but may protect the achene from desiccation or overheating, or enhance dispersal (see discussion of ecology, below).

The two varieties of *A. sphaerocephalus* differ only in that stems and leaves of var. *sphaerocephalus* are typically glabrous, or some

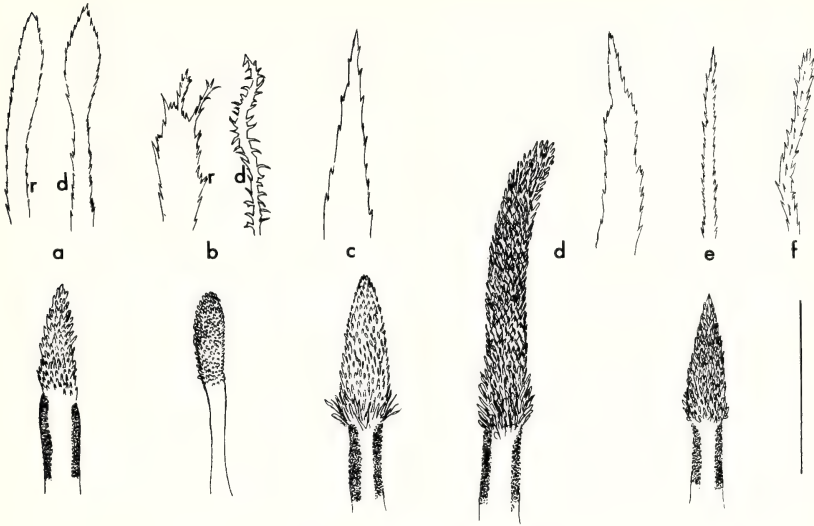


FIG. 4. Line drawings (traced from scanning electron micrographs) of pappus-member apices (above; r = ray, d = disk) and disk style-branch appendages (below): a. *Acamptopappus shockleyi* (style-branch appendage: Henrickson 9584, TEX; pappus member: Clokey 8157, TEX); b. *Amphipappus fremontii* var. *fremontii* (Cronquist 10649, TEX); c. *Eastwoodia elegans* (Eastwood and Howell 5791, TEX); d. *Vanclevea stylosa* (Shultz and Shultz 7393, COLO); e. *Ericameria cooperi* subsp. *cooperi* (Gierisch and Esplin 3460, COLO); f. *Stenotus acaulis* (Weber and Salamun 12568, COLO). Scale bar = 1 mm.

plants may have a very few, scattered trichomes on the leaf margins, whereas herbage of var. *hirtellus* is scabro-hirtellous (Blake 1929). This is a minor difference, although there is a geographic component to the variation (Fig. 2). Some populations in Los Angeles and San Bernardino cos., California, which lie in the area of overlap of the ranges of the varieties, have individuals with and without the vestiture. There are no intermediate individuals, either in these populations or elsewhere. This situation is parallel to that for the two varieties of *Amphipappus fremontii* (Porter 1943, Lane unpubl. data), in which var. *fremontii* is glabrous, and var. *spinosus* is scabro-hirtellous.

Ecology. *Acamptopappus* is well-adapted to the arid climate of the Mojave Desert. The leaves are drought-deciduous, and the white stems reflect sunlight. In favorable years, the plants are in leaf by February, have flowered by late March, and are in fruit by late April to early June (Ackerman et al. 1980, pers. obs.). In unfavorable years, plants often do not bloom at all, or the capitula wither before achenes are matured or even set.

Achenes are dispersed by wind and/or rain, being blown "tum-

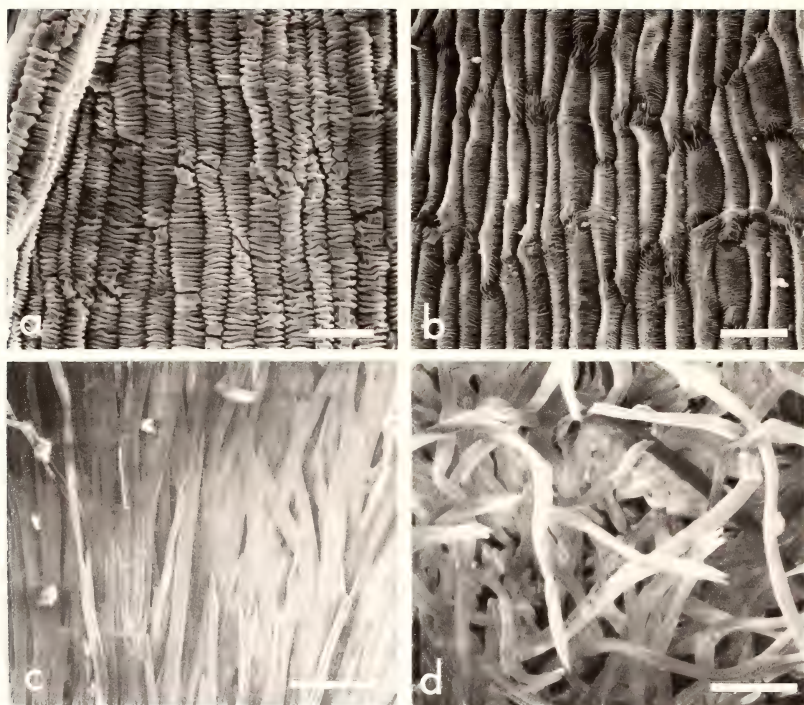


FIG. 5. Scanning electron micrographs of adaxial corolla epidermes and achene trichomes: a. disk corolla epidermis of *Acamptopappus sphaerocephalus* var. *sphaerocephalus* (M. E. Jones s.n., TEX); b. ray corolla epidermis of *A. shockleyi* (Henrickson 9584, TEX); c. achene trichomes of *Stenotus acaulis* (Weber and Salamun 12568, COLO); d. achene trichomes of *A. shockleyi* (Clokey 8157, TEX). Scale bar in a, b = 25 μ m; in c, d = 100 μ m.

bleweed style" or carried in runoff across the soil surface. The achenes are moved either individually or clustered by the interdigitation of their pappus members and achene trichomes. This dispersal syndrome, together with a seedling mortality of only 28% over eight years of study (Wallace and Romney 1980) may account for the finding of Wallace and co-workers (1980d) that *A. shockleyi* is usually found growing in clumps of several individuals, and of Wallace and Romney (1980) that the species is a pioneer that initiates new "fertile islands" in bare desert areas.

Acamptopappus shockleyi has been one among several subjects of a number of ecological and ecophysiological studies conducted on shrubby taxa of the Atomic Energy Commission (Nuclear Regulatory Commission) test site in southern Nevada (unfortunately, comparable data are not available for *A. sphaerocephalus*). Wallace et al. (1980d) found 28–101 plants per hectare, although the relative den-

sity of the species was less than 1% (El-Ghonemy et al. 1980c). The mean stem weight per plant in these studies ranged from 35.2 to 68.0 g (Bamberg et al. 1980, El-Ghonemy et al. 1980a, Wallace et al. 1980a). Plants are not particularly salt-tolerant (Romney and Wallace 1980). Seventy-five percent of the root mass usually lies within 20 cm of the surface (Wallace et al. 1980b) of soils that have relatively low cation exchange capacity, low exchangeable sodium, a medium amount of moisture retention, and low potassium content (El-Ghonemy et al. 1980b).

Phytochemistry. *Acamptopappus* produces sesquiterpenoids (C-15 compounds) and labdane diterpenoids (C-20 compounds). Eight compounds of the latter type that are new to science were isolated and characterized from *A. sphaerocephalus* by Jolad et al. (1988); these compounds were also found in *A. shockleyi*. The terpenoids of *Acamptopappus* (Jolad et al. 1988) are similar to those produced by other genera of the tribe Astereae, such as *Chrysanthamnus* and *Ericameria* (B. Timmermann pers. comm.).

Generic relationships. Distinguishing features of the two *Acamptopappus* species, *Amphipappus*, *Eastwoodia*, and *Vancleavea* (all monotypic) are presented in Table 1 and Fig. 4. I include *Amphipappus* in this discussion of the relationships of *Acamptopappus* because the two genera are placed near one another in floras (e.g., Keck in Munz 1959, Kearney and Peebles 1969), *Vancleavea* for the same reason and because of Steyermark's (1937) suggestion, and *Eastwoodia* because of its gross morphological similarity to these other genera. However, I suggest, based on the evidence presented below, that each of these genera is derived independently from an ancestral complex that also gave rise to *Chrysanthamnus*, *Ericameria*, and *Macronema* (*Haplopappus* sects. *Ericameria* and *Macronema* sensu Hall), which in turn have been considered related by Hall (Hall and Clements 1923, Hall 1928), and other authors.

Steyermark (1937) placed *Acamptopappus* near *Xanthisma* and distinguished it from *Grindelia* in his discussion of the relationships of the latter genus. I agree that *Acamptopappus* and *Grindelia* are very dissimilar, but *Acamptopappus* also differs from *Xanthisma* in many features, such as disk-corolla shape and epidermis pattern, style-branch appendage shape, leaf shape and vestiture, habit, habitat, and distribution. These three genera also differ in base chromosome number. All *Acamptopappus* taxa have $n = 9$ (Raven et al. 1960, Keil and Pinkava 1976, Pinkava and Keil 1977, Kovanda 1978, Schaak et al. 1982), *Grindelia* has $x = 6$, and *Xanthisma* has $x = 4$ (or possibly $x = 5$, see Semple 1976). All of the genera listed in Table 1, and *Chrysanthamnus*, *Ericameria*, and *Macronema*, have $x = 9$. Although chromosome number alone is insufficient evidence of relationship or lack thereof, the consistent correlation of mor-

phological characters with base chromosome number that is found in the Astereae supports its use as a character in a discussion such as this one.

Acamptopappus and *Amphipappus* are found in the Mojave and Sonoran deserts (Figs. 1, 2, and Porter 1943), and *Vanclevea* in the southeastern extension of the Great Basin desert in Utah and Arizona (Anderson and Weberg 1974). *Eastwoodia* occurs along the xeric western and southern rim of the San Joaquin Valley (Brandeggee 1894) on the eastern slopes of the South Coast Ranges and northern slopes of the Transverse Ranges of California (Lane in Hickman in prep.). All share certain features such as low, shrubby habit, greenish- or yellowish-white new growth, and white, sometimes varnished stems that become gray and shreddy with age.

Among the genera detailed in Table 1, *Acamptopappus* is most similar to *Amphipappus* (Fig. 3). Shared characters include those of the foliage, phyllary shape, color, and texture, disk-corolla shape, and the tortuous nature of the achene trichomes (Fig. 5d). These genera differ in capitulum size and shape, floret number, receptacle features, sexuality of the disk florets, style-branch appendage shape, pappus type, and degree of achene pubescence.

Steyermark (1937) saw a resemblance between *Eastwoodia* and *Acamptopappus* on the basis of receptacular projections between the florets. However, those of *Eastwoodia* are true paleae, whereas those of *Acamptopappus* are merely the extended rims of the alveolae. Both *Eastwoodia* and *Acamptopappus* have hermaphroditic disk florets and prominent ray florets in at least one taxon, but these are plesiomorphic conditions and therefore do not necessarily indicate relationship. Differences are found in the leaves, capitulum shape, phyllary shape and texture, disk-corolla shape, style-branch appendages and pappus type (Fig. 4), and degree of achene pubescence (Table 1).

Vanclevea differs from *Acamptopappus* in characters of the foliage, phyllaries, disk-corolla shape, style-branch appendages and pappus (Fig. 4), and degree of achene pubescence (Table 1). Very few similarities with *Acamptopappus*, except for those listed above for all four genera, can be found.

I suggest that although the four genera probably share a common heritage, they are independently derived because there are so few synapomorphies among them. Because each genus is so distinctive, indications of the nature of their common heritage must be sought in a large grouping of extant taxa. Of the Astereae genera that might be considered, the genera having $x = 9$ and comprising shrubby taxa of the southwestern deserts include *Chrysothamnus* (sensu Anderson 1984), *Ericameria* (sensu Urbatsch and Wussow 1979), and *Macronema* (= *Haplopappus* sect. *Macronema* sensu Hall 1928). *Petradoria* (sensu Anderson 1963) and *Stenotus* (*Haplopappus* sect. *Steno-*

tus sensu Hall 1928), although herbaceous, are nonetheless perennial with woody caudices and share general habitat preference and distribution with the other members of this alliance.

Many members of this group have greenish-white young stems that become white and then gray with shredding bark in age, as do all the genera of Table 1. Some members have the light green, non-resinous leaves of *Acamptopappus* and *Amphipappus*, and others have the dark green, resinous leaves of *Eastwoodia* and *Vancleavea*. A complete intergradation between the short, broadly funnelform disk-corolla shape of *Acamptopappus* and *Amphipappus* and the tubular-funnelform one of *Eastwoodia* and *Vancleavea* is found in this alliance as well.

The disk style-branch appendages of the *Chrysothamnus*–*Ericameria*–*Macronema* alliance, represented in Fig. 4e by that of *Ericameria cooperi*, are generally lanceolate-acute, although some species have more lanceolate ones. Those of *Acamptopappus* (Fig. 4a) are similar, whereas *Eastwoodia* (Fig. 4c) has broader ones, and *Vancleavea* (Fig. 4d) has the largest style-branch appendages of any taxon of Astereae that I have studied. *Amphipappus* (Fig. 4b) has lost female fertility in its disk florets, and this is reflected in absence of stigmatic lines on its style branches, which also have obtuse appendages. A reasonable interpretation of these data is that the style branches of *Amphipappus*, *Eastwoodia*, and *Vancleavea* are each, but separately, apomorphic with respect to those of the *Chrysothamnus*–*Ericameria*–*Macronema* alliance.

The pappus of members of this phylad is generally composed of barbellate bristles that are more or less round in cross section as are those of *Stenotus acaulis* (Fig. 4f), although *Ericameria cooperi* (Fig. 4e) and other members have flattened bristles. Porter (1943) suggested that the ray pappus of *Amphipappus* (Fig. 4b) is formed by fusion of bristles like those of the disk pappus (Fig. 4b) into scales. The same process, extended over evolutionary time, may account for the origin of the pappus scales of *Acamptopappus*, *Eastwoodia*, and *Vancleavea* (Fig. 4a, c, d) from those of ancestor(s) with broad, flat bristles such as those found in *Ericameria cooperi* (Fig. 4e) today. The pappus of *Amphipappus* (Fig. 4b) is always tortuous, but this may result from compression within the tightly imbricate involucre, much as the pappus of some florets within an *Acamptopappus* head may become twisted because it is compressed by surrounding florets during development. Thus, the similarity between these two genera with respect to tortuous pappus may be a parallelism rather than a synapomorphy.

Corolla epidermis patterns have been found to be useful characters at the generic and infrageneric levels in the Astereae (Lane 1982, 1985). *Acamptopappus*, *Amphipappus*, *Eastwoodia*, *Vancleavea*, *Chrysothamnus*, *Macronema*, and *Petradoria* have the same disk

corolla epidermis pattern (Fig. 5a). *Acamptopappus*, *Amphipappus*, and *Macronema* also share the same ray corolla epidermis pattern (Fig. 5b), whereas *Petradoria*, *Ericameria*, and *Stenotus* have a different one (Lane unpubl. data). It is difficult to polarize the epidermal pattern characters, but it would seem that one or the other of these two groups of three genera is synapomorphic in this respect.

It would be desirable to have a cladistic analysis of the relationships of the genera discussed above. However, to present a cladogram at this time would be premature because such an analysis requires that all taxa belonging to a lineage be included in the analysis. The scope of the current study has not ensured that this is the case; neither has it yet been possible to determine an appropriate out-group.

Future studies leading to thorough phylogenetic analysis have been designed to test the hypothesis that *Acamptopappus* has been derived from the ancestral complex that gave rise more directly to the *Chrysothamnus*–*Ericameria*–*Macronema* phylad. The single taxon of this group to which *Acamptopappus* is most similar is *E. parrasana*. With this species, *Acamptopappus* shares capitulum shape, phyllary features, and reflexing involucre in addition to the overall similarities of the genera given above. The similar but separate derivation of *Amphipappus*, *Eastwoodia*, and *Vanclevea* is another hypothesis to be tested in future. The distinctiveness of *Acamptopappus* and each of these genera may be accounted for by elapsed time since separation of the lineages, and the strong selection pressures of their desert habitats.

TAXONOMIC TREATMENT

Acamptopappus (A. Gray) A. Gray. Proc. Amer. Acad. Arts 8:634. 1873.—*Aplopappus* Cass. sect. *Acamptopappus* A. Gray, Mem. Amer. Acad. Arts (ser. 2) 4:76 [Pl. Fendler. 76]. 1849.—TYPE: *Acamptopappus sphaerocephalus* (Harv. & A. Gray in A. Gray) A. Gray.

Shrubs to 4 dm high, scraggly or rounded (Fig. 3); taproots woody, vertical or usually laterally spreading; stems decumbent, divergent or erect, striate; young stems greenish-white or -yellow, becoming white; old stems gray, usually with shredding bark; leaves pale green to light gray-green, borne singly, rarely in axillary fascicles below, spreading-ascendent to appressed-erect, linear to lanceolate or narrowly obovate or spatulate, 1-nervate, entire, glabrous or scabro-hirtellous at margins, generally minutely spinulose at apices, glabrous or scabro-hirtellous on both surfaces; capitula borne singly or occasionally in cymose clusters; buds expanding rapidly just prior to anthesis; involucre broadly campanulate-hemispheric to nearly spheric; phyllaries in 2–3 series, broadly ovate to ovate-elliptic, chartaceous, brittle, cream-yellow at bases, green at apices, with broad,

scarious, erose margins, all distinctly reflexing at maturity to release achenes; receptacle deeply alveolate, with projections between florets but not chaffy; heads radiate or eradiate, corollas yellow; disk corollas broadly funnellform, sinuses deep, lobes spreading to reflexed; style-branch-appendages narrowly triangular-lanceolate (Fig. 4a), somewhat exceeding the stigmatic portion; achenes obconic, extremely densely long-villous; trichomes white, bronze, rufous, or brownish, outer straight, inner contorted or tortuous (Fig. 5d); pappus of 1-seriate, white, scarcely erose scales with acute-lanceolate to narrowly spatulate apices (Fig. 4a), slightly exceeding achenes; base chromosome number: $x = 9$. Flowering (Mar-)Apr-May(-Jun) (Ackerman et al. 1980, Lane hoc. loc.).

KEY TO TAXA OF *Acamptopappus*

1. Heads radiate, involucre campanulate to hemispheric *A. shockleyi*
1. Heads eradiate, involucre hemispheric to globose.
 2. Stems and leaves scabro-hirtellous *A. sphaerocephalus* var. *hirtellus*
 2. Stems and leaves glabrous, or only leaf margins scabro-hirtellous *A. sphaerocephalus* var. *sphaerocephalus*

Acamptopappus shockleyi A. Gray, Proc. Amer. Acad. Arts 17:208. 1882. — TYPE: USA, Nevada, Esmeralda Co., Candelaria, 1881, *Shockley 34* (GH!).

Stems decumbent to ascendent, (1.5-)2-3(-3.3) dm, usually spinescent with age, surfaces usually scabro-hirtellous; leaves spreading-ascendent, narrowly obovate to narrowly spatulate, (0.7-)1-1.6 (-2) cm long, (2-)3-4(-5) mm wide, scabro-hirtellous; capitula borne singly; involucre campanulate to hemispheric, 7-11(-13) mm high, (10-)13-19 mm wide; phyllaries 13-18(-23), (3.5-)5-9(-11) mm long, (1.8-)2-4(-6) mm wide; ray florets 5-14, corollas (3.5-)6-17(-19.5) mm long, (1.5-)2.5-6.5 mm wide; disk florets 30-80, corollas (2.3-)3.2-5(-5.5) mm high; achenes (1-)1.5-3.5(-4.7) mm long, (0.4-)0.8-1.8(-2.9) mm wide; pappus scales (15-)18-30(-38), less spatulate in rays than disks, (2.7-)3-4.5(-5) mm high.

Distribution and habitat. Mojave Desert areas of southeastern California and southern Nevada (Fig. 1); 500-2000 m. Mesas, slopes, ravines, and washes in *Larrea* and *Yucca brevifolia* communities, in association with *Atriplex*, *Amphipappus*, *Artemisia*, *Lycium*, *Grayia*, *Encelia*, *Psilostrophe*, *Thamnosma*, *Hymenoclea*, *Eurotia*, and/or *Hilaria*.

Comments. Gray's (1882) description of *A. shockleyi* was based on a specimen numbered *Shockley 34*, collected in 1881. Other

specimens with this number are at CAS and UC (but these are from Rhyolite or Tonopah and dated 1883 or 1907), and another at NY (dated 1886). Clearly these specimens cannot be considered isotypes, though the NY specimen presumably is a topotype. Isotypic status for a sheet at RSA is doubtful because it gives only "Apr-May" for collection date, even though it bears the correct locality and number. Given Shockley's re-use of the number 34, I doubt that it was collected in 1881.

Representative specimens. USA, California, Inyo Co., Payson Canyon, White Mts., 14 Jun 1932, *Duran 3295* (CAS, NY, GH, F, MO, NY, RM, RSA, UC, US, UTC). San Bernardino Co., 4 mi e. of Horse Spring, Mojave Desert, Kensington Mts., 15 May 1935, *Wolf 6848* (CAS, COLO, MO, NY, RSA, UC). Nevada, Clark Co., Old Kyle Canyon fan, 11 May 1938, *Clokey 8157* (ARIZ, CAS, F, GH, K, MO, NY, RM, RSA, SD, TEX, UC, UTC). Esmeralda Co., Candelaria, 22 Jun 1882, *Jones 3895* (CAS, F, MO, NY, POM, RSA, NY, UC, UTC). Lincoln Co., 11 mi s. of Alamo, 6 Apr 1934, *Maguire et al. 5033* (GH, MO, RM, UC, UTC). Mineral Co., near Mina, 5 Jun 1906, *Heller 8368* (CAS, F, GH, MO, NY, US). Nye Co., Smokey Valley, 9 Jun 1945, *Maguire and Holmgren 25362* (ARIZ, GH, NY, US, UTC).

Acamptopappus sphaerocephalus (Harvey & A. Gray in A. Gray) A. Gray.

Stems usually many, much-branched, ascendent to erect, (1.5-)2-3.5(-4) dm, with surfaces scabro-hirtellous or glabrous; leaves ascendent-appressed, linear to narrowly oblanceolate, 0.5-2(-2.8) cm long, (1-)1.5-3(-4) mm wide, scabro-hirtellous or glabrous; capitula very numerous, borne singly or in clusters; involucre hemispheric to spheric, 4-7 mm high, (1.5-)6-11 mm wide; phyllaries 11-18(-20), (2.5-)3.2-5.5(-6.5) mm long, (1.5-)1.9-3(-3.6) mm wide; heads eradiate; disk florets (13-)14-24(-27), corollas (2.1-)2.5-4.3(-4.7) mm high; achenes (1.2-)1.7-3.3(-3.7) mm high, (0.6-)0.8-1.9(-2.2) mm wide; pappus bristles (15-)17-26(-28), (1.7-)2.1-3.7(-4.4) mm high, apices narrowly spatulate.

Distribution and habitat. Mojave and Sonoran desert areas of southern California, southern Nevada and Utah, and south-central Arizona (Fig. 2); 5-2000 m. Gravelly, rocky soils on slopes and flat areas in grasslands, deserts, and *Juniperus* woodlands; in association with *Larrea*, *Yucca*, *Viguiera*, *Eriogonum*, *Salsola*, *Ambrosia*, *Artemisia*, *Chrysothamnus*, *Coleogyne*, *Ephedra*, *Canotia*, *Hymenoclea*, *Cercidium*, *Fouquieria*, *Carnegia*, *Opuntia*, and/or *Ferocactus*.

Comments. Some populations in the area of overlap of the two varieties of this species (Fig. 2) are mixed with respect to the distinguishing pubescence character. Representative collections from

this area include: California, Los Angeles Co., Lancaster, Jun 1902, *Elmer 3621* (CAS, F, GH, K, MO, NY, RSA, US). San Bernardino Co., Mojave Desert, May 1882, *Parish and Parish 139* (CAS, F, GH, MO, NY, SD, UC, US); Cima, Mojave Desert, Jun 1915, *Brandegee s.n.* (F, GH, MO, NY, RM, UC); Mojave Desert, Spring 1927, *Hutchinson s.n.* (LL, TEX).

Populations of *A. sphaerocephalus* may very rarely contain individuals with vestigial ray florets (D. Keil pers. comm., M. Lane pers. obs.). This condition might result from one of two phenomena: 1) hybridization with the radiate *A. shockleyi* or 2) partial expression of ray-floret genes that were suppressed during the evolution of *A. sphaerocephalus* from a radiate ancestor. Either explanation is plausible, but neither is more strongly supported than the other by evidence available at this time. There are infrequent cases of co-occurrence of the two *Acamptopappus* species where their ranges overlap (Figs. 1, 2) and hybridization may occur, although I have seen no specimens that I would suspect to be of hybrid origin. Vestigial rays occasionally occur in eradiate taxa of other genera of Astereae that I have studied (for example, *Isocoma*), indicating that loss of rays is an apomorphic condition but that their suppression is not absolute.

Acamptopappus sphaerocephalus (Harv. & A. Gray in A. Gray) var. *hirtellus* S. F. Blake, J. Wash. Acad. Sci. 19:270. 1929.—TYPE: USA, California, Inyo Co., near Lone Pine, 7 Jun 1891, *Coville and Funston 890* (US!).

Stems (1.5–)2.5–3.3(–3.8) dm high, scabro-hirtellous; leaves (0.6–)0.8–1.3 cm long, 1.5–3(–4) mm wide, scabro-hirtellous; involucre 6–7 mm high, (1.5–)8–11 mm wide; phyllaries (14–)15–18(–20), (2.8–)3.7–5.4(–5.7) mm long, (1.5)2–2.8(–3.1) mm wide; disk florets (13–)16–24(–27), corollas 2.8–3.6(–4.5) mm high; achenes 1.7–3.2(–3.7) mm long, 0.7–1.7(–2.2) mm wide; pappus bristles 15–24, (2.1–)2.8–3.3(–3.7) mm high. Gravelly soils in deserts and *Juniperus* woodlands; 5–1600 m.

Representative specimens. USA, Arizona, Mohave Co., Fort Mohave, Apr 1884, *Lemmon s.n.* (UC, US). California, Inyo Co., Alabama Hills, 3 mi w. of Lone Pine, 23 May 1958, *Rose 58061* (CAS, COLO, GH, JEPS, NY, RSA, US). Kern Co., near Searles, 28 May 1932, *Duran 3224* (CAS, COLO, F, GH, MO, NY, RM, RSA, UC, UTC, US). Los Angeles Co., near Lancaster, 11 Jun 1906, *Hall and Chandler 7388* (ARIZ, F, K, MO, NY, RM, RSA). San Bernardino Co., Mojave River district, Apr [or 23 May or 1 Jun?] 1876, *Palmer 219* (F, MO, NY, US). Nevada, Clark Co., 15 mi e. of Glendale, 19 May 1933, *Maguire and Blood 4487* (MO, RM, RSA, UC, UTC). Lincoln Co., Moapa, 12 May 1905, *Kennedy 1077* (F).

Acamptopappus sphaerocephalus (Harv. & A. Gray in A. Gray) A. Gray var. *sphaerocephalus*, Proc. Amer. Acad. Arts 8:634. 1873.—*Haplopappus sphaerocephalus* Harvey & A. Gray in A. Gray, Mem. Amer. Acad. Arts, ser. 2, 4:76 [Pl. Fendler. 76]. 1849.—TYPE: USA, California, [San Diego Co.?], [without locality], [1832], Coulter s.n. exsic. no. 281 (GH!; isotypes K!, TCD!).

Stems (1.8–)2.4–3.5(–3.8) dm high, glabrous; leaves (0.5–)1–2(–2.8) cm long, (1–)1.5–3(–4) mm wide, glabrous; involucre 4–7 mm high, (1.5–)6–10 mm wide; phyllaries 11–18(–19), (2.5–)3.2–5.3(–6.4) mm long, 1.9–3(–3.6) mm wide; disk florets (13–)14–22(–26), corollas (2.1–)2.5–4.3(–4.7) mm high; achenes (1.2–)1.7–3.2(–3.7) mm long, (0.6–)0.8–1.9(–2.2) mm wide; pappus scales (15–)17–28, (1.7–)2.1–3.7(–4.4) mm high. Gravelly, rocky soils in grasslands, deserts, and woodlands; 60–2000 m.

Comments. Coulter's specimen bears no date, but it probably was collected sometime during his excursion from Monterey to Yuma, Arizona, by way of San Diego, between 20 March and 19 July 1832 (Coville 1895, McKelvey 1955). The route followed by Coulter's party (Fig. 2) passed through or near three possible collection areas. 1) Northeastern Los Angeles Co. According to Coville (1895), the route was on the southwestern side of the San Gabriel Mountains, between San Fernando and San Gabriel. The only known localities for *A. sphaerocephalus* in or near the San Gabriels (Pallett Creek, Little Rock Creek, and Bob's Gap) are on the northeastern side of the mountains. 2) East-central San Diego Co. Coulter passed through either the San Felipe Valley or the next valley south between 30 April and 8 May, and again between 17 and 27 May on the return trip (Coville 1895). There are a number of specimens from this area, and the dates of Coulter's visit during the outbound trip coincide with those for collections that are in the same state of maturity as the type. 3) Area of Yuma, Arizona. Coulter was in this area 8 through 17 May (Coville 1895); however, specimens from that portion of the range of the species have completely mature achenes by that date, and the type specimen has only partially mature achenes. This information suggests that the type locality is one of the valleys of east-central San Diego Co.

Representative specimens. USA, Arizona, Coconino Co., Glen Canyon National Recreation Area, Glen Canyon, ca. 1 mi due s. of Wahweap Marina, 26 May 1983, *Welsh 22066* (BRY, RM). Gila Co., between Roosevelt Dam and Tonto Basin, 15 May 1935, *Nelson and Nelson 1933* (GH, K, MO, NY, RM, UC, US, UTC). Graham Co., 2 mi below San Juan Mine, Gila Mts., 8 Apr 1935, *Maguire and Maguire 10546* (ARIZ, GH, MO, NY, UTC). La Paz Co., 1 mi s. of Alamo State Park boundary on road to Wenden, 10 Mar 1973,

McLeod and Pinkava 10326 (ARIZ, ASU, LL, NY, SD, TEX). Maricopa Co., roadside s. of Cañon, 21 Apr 1938, *Foster and Arnold 338* (CAS, GH, UC, US). Mohave Co., Yucca, 15 May 1884, *Jones 3911* (ARIZ, CAS, F, GH, POM, RM, UC, US, UTC). Pima Co., Walls Well, Organ Pipe Cactus National Monument, 28 Apr 1939, *Nichol s.n.* (ARIZ). Pinal Co., Camp Grant, 14 May 1867, *Palmer 114* (GH, MO). Yavapai Co., Black Canyon P.O., 14 Apr 1960, *Demaree 42241* (ARIZ, NY, TEX). Yuma Co., Yuma, 21 Apr 1938, *Crooks and Darrow s.n.* (ARIZ, NY). California, Imperial Co., Mountain Springs Grade, 17 Apr [without year], *Orcutt s.n.* (UC). Inyo Co., Dante's View above Death Valley, 11 Jun 1930, *Peebles 302* (ARIZ, NY). Kern Co., 8 mi ne. of Mojave, 12 May 1930, *Howell 4913* (CAS). Los Angeles Co., Pallett Creek, San Gabriel Mts., 27 May 1923, *Munz 6896* (CAS, NY, RSA). Riverside Co., San Jacinto Mts., e. base along the borders of the Colorado Desert, Jun 1901, *Hall 2108* (CAS, K, MO, NY, POM, UC, US). San Bernardino Co., Baker, Mohave Desert, 2 May 1933, *Jones s.n.* (GH, K, RM, RSA, UC, UTC). San Diego Co., Yaqui Wells, Colorado Desert, 14 Apr 1913, *Eastwood 2800* (CAS, GH, K, NY, US). Nevada, Clark Co., St. Thomas Gap area sw. of Whitney Ridge, 0.9 road mi n. of Grand Gulch Rd on Reservoir Rd, 14 May 1982, *Tiehm 6867* (MO, RSA, UTC). Lincoln Co., Moapa, 5 May 1909, *Kennedy 1808* (F). Utah, Kane Co., ca. 2 mi s. of Nun Butte, ca. 20 mi e. of Glen Canyon City, 24 May 1972, *Atwood 4062* (MO, US). Washington Co., e. slope of Black Hill, St. George, 24 May 1942, *Gould 1772* (CAS, COLO, F, GH, NY, POM, UC, UTC).

EXCLUDED TAXON

Acamptopappus microcephalus M. E. Jones, Contr. W. Bot. 8:33. 1898. = *Ericameria cooperi* (A. Gray) H. M. Hall subsp. *cooperi*.

ACKNOWLEDGMENTS

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ANNOUNCEMENT

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GENECOLOGY OF *CERASTIUM ARVENSE* AND
C. BEERINGIANUM (CARYOPHYLLACEAE)
IN NORTHWEST WASHINGTON

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ABSTRACT

From principal components analyses, patterns of morphological variation were determined in and among three populations of *Cerastium arvense* and one population of *C. beeringianum*, under both field (natural) and garden conditions. The three populations of *C. arvense* occurred at near sea level, mid-montane and alpine elevations, respectively. The *C. beeringianum* population was also alpine and occurred on a serpentine substrate, as did the mid-montane population of *C. arvense*. The analyses showed considerable phenotypic plasticity in non-serpentine populations, much less in serpentine populations. There appeared to be little genetic differentiation in *C. arvense* along the elevational gradient, except for a more or less persistent cushion habit in the alpine population. The two closely related species overlapped morphologically but could be separated by variables used, especially when grown under garden conditions.

Cerastium arvense was described as "one of the most perplexing species in our range" by Hitchcock et al. (1964). They noted further that *C. beeringianum* cannot be satisfactorily separated from *C. arvense* in the high Cascades where the characteristics of the two taxa tend to merge. According to Hultén (1956) these species hybridize in Newfoundland and Labrador and are part of a large polyploid complex united by introgressive hybridization. Chromosome numbers of most members of the complex are known (Sollner 1954, Brett 1955, Ugborogho 1973, 1977). Ploidy of *C. arvense* varies but appears to be diploid ($2n = 36$) throughout the Pacific Northwest, whereas *C. beeringianum* is a tetraploid ($2n = 72$). Meiotic regularity and high pollen viability provide evidence that *C. beeringianum* is a stable allotetraploid.

Interspecific hybridization in Hultén's complex has undoubtedly been facilitated by reproductive biology. At least *C. arvense* is an obligate outcrosser that requires insect pollination for successful seed set (Ugborogho 1977); and both taxa have open, bowl-shaped flowers that provide easy access to pollen and nectar rewards by insects. The

generalist pollination strategy of the two species has been substantiated (Ugborogho 1977, Arroyo et al. 1982, Shaw and Taylor 1986).

Cerastium arvense is widely distributed, both geographically and altitudinally. In the Pacific Northwest it ranges from rocky, exposed coastlines to alpine ridges. *Cerastium beeringianum*, on the other hand, has a restricted distribution in the Northwest, occurring in a few alpine locations. The purpose of our study, then, was two-fold: (1) to examine the patterns of variation within and among geographically and elevationally disjunct populations of *Cerastium* and to ascertain the extent to which observed variation was the result of phenotypic plasticity and to what extent it is genetically fixed; (2) to confirm the taxonomic distinction of an alpine population thought to be *C. beeringianum* and to compare patterns of variation of this population to those of *C. arvense*.

METHODS

Four sites varying in climate, elevation, and edaphic conditions were chosen for study. These sites (Deception Pass, Sumas Mountain, the Twin Sisters, and Chowder Ridge) are shown in Fig. 1 and general descriptions are given in Table 1. Detailed descriptions of the climate and geology relating to the four sites are available from Moen (1962), Phillips (1966), and McKee (1972). Taylor and Douglas (1978) described the natural history of Chowder Ridge, and Kruckeberg (1969) published a detailed account of vegetation occurring on serpentine soils in the northwest, including Sumas Mountain and the Twin Sisters.

Sampling and collection. At Deception Pass, Chowder Ridge, and the Twin Sisters *Cerastium* populations were large and the plants occurred in diverse habitats. To effectively sample the variation of these populations, we positioned four widely separated, 55 m transects parallel to the slope; the sum of the transect length was therefore 220 m. Ten specimens were collected at 20 m intervals along the total transect length. Because the *Cerastium* population at Sumas Mountain was smaller and more limited in distribution, seven shorter (20–55 m) transects were established, again with a total length of 220 m. Ten specimens were also collected at 20 m intervals along this total transect length. From each of the 40 specimens collected, three mature flowers with non-dehiscid anthers were selected for pollen analysis, and plants were pressed for subsequent morphological analyses. These collections were made in the summer of 1983.

Also during the summer of 1983, 40 cuttings were collected at 5 m intervals along the transects at each study site. These were propagated in a potting mixture of one part each mineral soil (taken from respective study sites), peat, and perlite. In 1984 an additional 20 cuttings were similarly collected from each study site and prop-

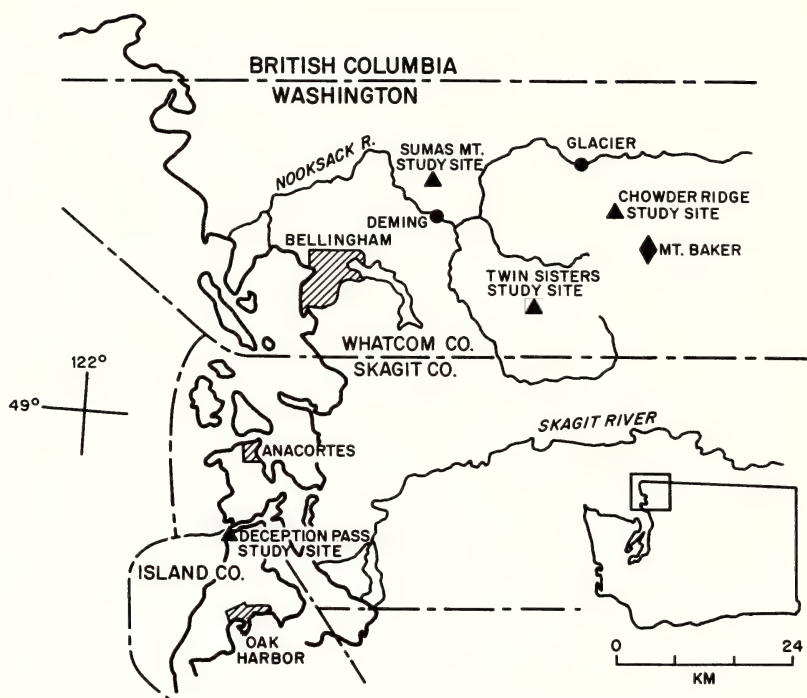


FIG. 1. Location of the four populations (triangles) of *Cerastium* studied in North-west Washington. The Twin Sisters population = *C. beeringianum*.

agated in a mixture of one part each sand, peat, and perlite. All cuttings were protected from direct sunlight until new growth was observed, then transferred to an experimental garden at Western Washington University. In June 1985, 10 mature specimens were randomly collected from each of the four transplanted populations and pressed.

Pollen analysis. The flowers sampled for pollen analysis were stored at 5°C until slides could be prepared using a technique adapted from Ugborgho (1973). Two anthers from each of the three flowers were squashed in a 1% acetocarmine and glycerine solution. The stained mounts were allowed to set for 24 hours before being examined. This enabled the pollen grains to absorb the stain and stabilize in size. Using a calibrated stage, each slide was then divided into quadrats and 25 pollen grains were observed from each quadrat. Pollen grains that were swollen and deeply stained were scored as viable. In addition, every tenth pollen grain was measured using a calibrated ocular.

Morphometric analysis. Twenty-three morphologic and pollen variables were chosen for analyses. These are listed in Tables 2 and

TABLE 1. ENVIRONMENTAL CONDITIONS OF STUDY SITES.

Location	Elevation (m)	Mean annual precipita- tion (cm)	Topography	Aspect	Soil parent materials
Deception Pass	sea level-148	51	gentle coastal bluff to steep rock outcroppings	se.	marine sediments
Sumas Mountain	799-832	179	steep non-forested rock outcroppings	ene.	serpentine
Twin Sisters	1665-1831 (alpine)	279	steep rocky slope	nw.	serpentine
Chowder Ridge	2200-2300 (alpine)	305	steep rocky slope	sse.	marine sediments and andesite

TABLE 2. VARIABLES USED IN PRINCIPAL COMPONENTS ANALYSES. Factor loadings are given for the first and second principal components of 40 field, 40 garden, and 80 field + garden (fld + gard) specimens. Variables making a relative contribution of more than 0.5 to indicated component(s) have been highlighted. Signs of the loading values have been disregarded.

	Factor 1			Factor 2		
	Field	Garden	Fld + gard	Field	Garden	Fld + gard
Distance between bracts and first leaves (mm)	0.85531	0.76875	0.73369	0.30934	0.19163	0.45323
Length of the flowering stem (cm)	0.84327	0.88889	0.76201	0.31695	0.18310	0.52825
Length of the upper internodes (mm)	0.77374	0.89845	0.57964	0.54616	0.02423	0.66768
Mean pollen diameter	0.73230	0.26002	0.61612	0.31551	0.58208	0.42545
Number of cymes per inflorescence	0.69873	0.23644	0.61788	0.26480	0.54087	0.07718
Length of the first leaf below the bracts (mm)	0.68615	0.82621	0.60270	0.22297	0.06093	0.49596
Length of petals (mm)	0.68439	0.01570	0.67515	0.09721	0.61116	0.14408
Length of the second internodes (mm)	0.67764	0.86001	0.46378	0.60301	0.12896	0.72235
Length of pubescence on the stem below bracts (mm)	0.65416	0.17521	0.50870	0.31993	0.60825	0.42931
Width of first leaf below bracts (mm)	0.58926	0.11077	0.70397	0.60974	0.81121	0.41151
Width of bracts (mm)	0.52118	0.10492	0.66511	0.66289	0.79813	0.42235
Number of flowers per cyme	0.50590	0.69438	0.58527	0.19893	0.15764	0.36709
Length of bracts (mm)	0.49922	0.32695	0.59338	0.59825	0.50183	0.19834
Number of sterile shoots in leaf nodes	0.49479	0.63240	0.31098	0.06596	0.26307	0.45527
Length of sepals (mm)	0.47757	0.12228	0.42661	0.05385	0.61544	0.01778
Width of scarious margin on bracts (mm)	0.42967	0.53107	0.26783	0.64410	0.35616	0.64449
Length of pubescence on sepals (mm)	0.31036	0.19523	0.49227	0.14782	0.70497	0.36552
% Pollen stainability	0.19889	0.24509	0.13902	0.25684	0.37802	0.32604
Depth of petal lobes (mm)	0.18227	0.22543	0.16280	0.09695	0.09069	0.22467
Width of petals (mm)	0.18076	0.31942	0.39034	0.23087	0.30361	0.01381
Number of leaf nodes per flowering stem	0.15376	0.23292	0.12658	0.10920	0.16282	0.24841
Width of sepals (mm)	0.11708	0.05953	0.38792	0.60662	0.60119	0.36864
Standard deviation of pollen diameter	0.10512	0.02354	0.00308	0.11044	0.06818	0.07039

TABLE 3. MEAN VALUES OF VARIABLES OF FIELD VERSUS GARDEN SPECIMENS IN EACH OF THE FOUR POPULATIONS. Those values which are significantly different at a 5% level are highlighted.

Variable	Deception Pass		Sumas Mountain		Twin Sister		Chowder Ridge	
	Field	Garden	Field	Garden	Field	Garden	Field	Garden
Inflorescence								
Number of cymes	2.4	2.8	2.6	1.7	2.5	2.7	1.4	2.9
Number of flowers per cyme	1.4	2.2	1.3	1.7	1.3	1.5	1.0	1.6
Corolla								
Length of petals (mm)	8.5	10.9	10.1	9.5	9.9	11.4	8.3	10.5
Width of petals (mm)	4.4	5.4	4.1	4.1	4.2	4.5	4.3	5.1
Depth of petal lobes (mm)	2.3	2.8	2.1	2.5	2.8	3.0	2.3	2.7
Pollen								
% Pollen stainability	83.1	72.8	75.3	66.1	83.9	89.9	71.6	80.2
Mean pollen diameter (mm)	36.1	38.1	36.2	36.7	39.7	43.5	33.0	37.6
Standard deviation	2.3	2.1	2.8	2.8	2.6	2.5	2.4	2.6
Calyx								
Length of sepals (mm)	4.7	5.3	6.1	5.1	5.9	5.5	4.7	5.7
Width of sepals (mm)	1.7	1.8	1.6	1.7	1.9	2.0	1.7	2.2
Length of pubescence on sepals (mm)	0.4	0.6	0.4	0.3	0.4	0.9	0.3	0.4
Leaves								
Length of bracts (mm)	3.6	6.9	4.3	4.0	6.3	5.1	3.8	5.3
Width of bracts (mm)	1.7	2.9	1.6	1.8	3.3	3.6	1.8	3.4
Width of scarious margin on bracts (mm)	0.5	0.4	0.4	0.4	0.1	0.1	0.4	0.5
Length of first leaf below bracts (mm)	8.1	16.6	15.1	13.3	10.9	8.6	8.4	12.8
Width of first leaf below bracts (mm)	2.1	3.6	2.2	2.5	4.6	4.9	2.6	5.0
Number of sterile shoots in leaf nodes	9.9	8.6	6.0	6.2	3.8	3.6	9.5	5.2
Stem								
Length of flowering stem (cm)	12.6	28.1	17.2	13.7	13.9	12.3	6.8	16.0
Number of leaf nodes per flowering stem	9.4	6.2	6.7	6.3	8.4	5.8	7.7	5.0
Distance between bracts and first leaves (mm)	25.5	64.5	8.9	32.8	42.6	31.5	10.7	46.8
Length of pubescence on stem below the bracts (mm)	0.5	0.6	0.5	0.4	0.6	0.8	0.4	0
Length of upper internodes (mm)	17.5	27.5	29.3	17.4	19.8	11.4	7.4	18.8
Length of second internodes (mm)	12.2	18.0	17.4	11.8	11.7	4.9	6.2	11.8

3 and were used in principal components analyses available through Nie et al. (1983). In addition, a t-test of independent means was used to compare the intrapopulation variation between garden and field collections from each of the four locations. The significance level was established at $p \leq 0.05$.

RESULTS

Transplant establishment. Between 25 and 41% of the cuttings survived transplantation. Survival rates during the several months that the plants were maintained in the pots depended on the population source and potting mixture. Plants from Chowder Ridge and Deception Pass exhibited apparent preference for soil mixtures containing sand rather than native soil. In contrast, plants from the serpentine populations fared significantly better when propagated in mixtures containing native soils.

Following transplantation from the pots into the garden, the plants readily became established and formed mats up to 83 cm in diameter by the end of the second year. During the second year the garden transplants flowered and successfully set seed. As shown in Fig. 2, the low elevation field populations flowered earlier in the season than did the alpine populations. However, garden transplants flowered simultaneously regardless of their source.

The requirements for seed germination were less uniform. Seeds from Deception Pass and Sumas Mountain transplants germinated within ca. 14 days on moistened filter paper at 5°C, whereas low germination rates were observed for alpine transplants.

Factor analyses. Analyses involving variables listed in Table 2 were used to quantify intra- and interpopulational variation, to establish relationships among populations, and to determine the extent to which observed variation was due to phenotypic plasticity. Figure 3 is a two-dimensional ordination produced from a principal components analysis (PCA) of the 40 field specimens. This analysis revealed variation within each population and overlap among populations. Forty-one percent of the variance was accounted for by the first two components. Characters that received high loading on the first component were those involving overall size, inflorescence, and pollen diameter. Characters that described bract shape, and width of the scarious bract margin received high loadings on the first and second components. Factor loadings for the 23 variables in this and subsequent PCA's are given in Table 2.

As reflected in the PCA ordination of Fig. 4, interpopulational variation was reduced in garden transplants, especially between the Deception Pass and Sumas Mountain populations. The distinction between the Twin Sisters population, which ultimately proved to be *C. beeringianum*, and other, *C. arvense*, populations was rather sharp.

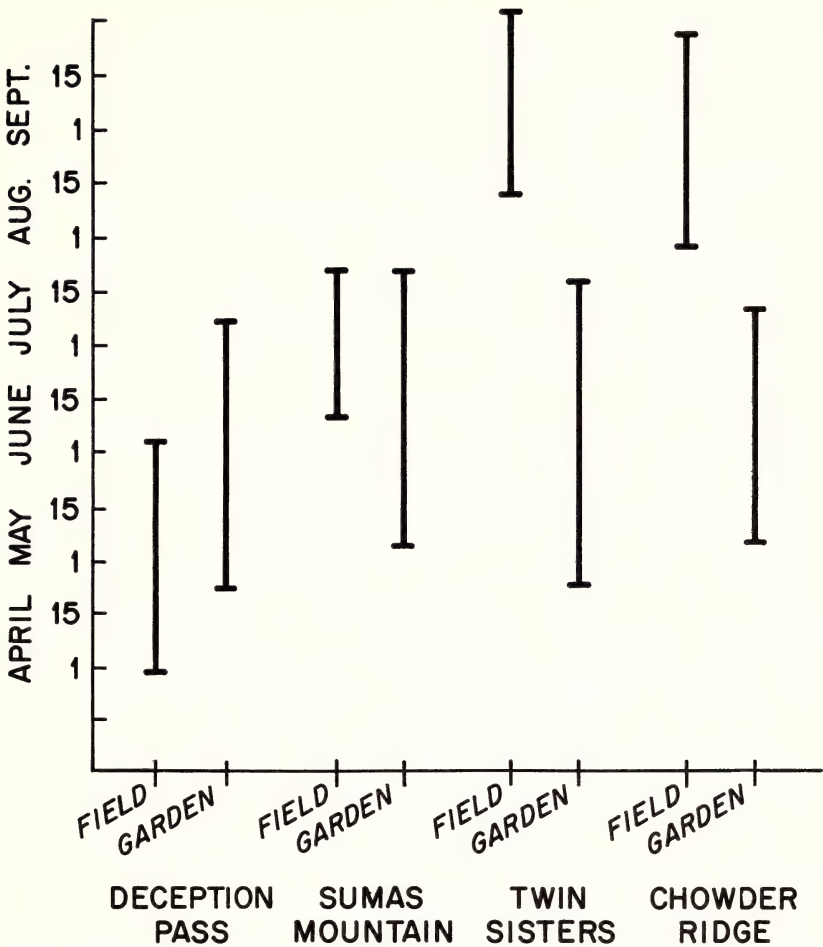
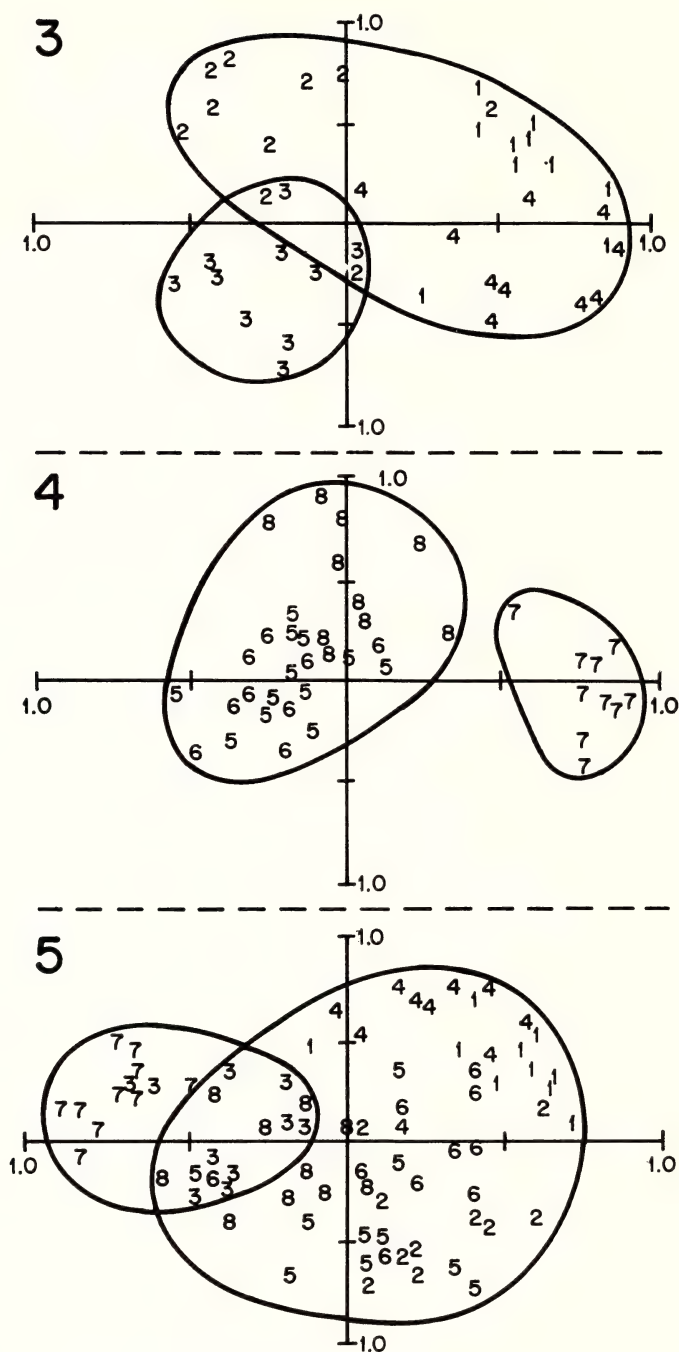


FIG. 2. Flowering period for field populations of *Cerastium* and garden transplants.

In this analysis 35% of the variation was accounted for by the first and second components. Characters that described the overall height of the plants, the number of sterile shoots, and the width of the scarious bract margin had high loadings on the first component and therefore differed between species. Characters describing the shape of the bracts and the width of the leaves received high loadings on the second component (Table 2).

A PCA ordination of the combined field and garden data sets (Fig. 5) indicates considerable overlap among the populations. There is little differentiation between field and garden populations from the Twin Sisters and from Sumas Mountain. However, field and garden



populations from the non-serpentine sites, Chowder Ridge and Deception Pass, clustered separately. This suggests that plants of the latter sites exhibited greater phenotypic plasticity. In Fig. 5 the first and second principal components accounted for 42% of the variance. Morphological complexes that described plant height, leaf width, and the inflorescence received high loading on the first component and were therefore important in separation of the Twin Sisters population and, to a lesser extent, the Chowder Ridge field population from other populations. Plant height, the width of the scarious margin on the bracts and the number of sterile shoots at the leaf nodes received high scores on the second component and thus were important in separating the field from the garden populations from Chowder Ridge and, especially, Deception Pass. Factor loadings are given in Table 2.

To determine extent of variation due to phenotypic plasticity, the independent means of variables of field and garden specimens were compared (Table 3). The number of variables that differed significantly between field and garden specimens was: 17 from the Chowder Ridge population, 14 from Deception Pass, 6 from the Twin Sisters, and 5 from Sumas Mountain. This strongly suggests that the Chowder Ridge and Deception Pass populations expressed more phenotypic plasticity than did the populations occurring on serpentine substrates. The most plastic variables were length of internodes, distance between bracts and first leaves, number of nodes, length of pubescence, and pollen diameter. These variables varied significantly between field and garden specimens from at least three of the four populations (Table 3). The least plastic variables were those describing flowers, width of the scarious margin of bracts, leaf width, number of sterile shoots, and pollen stainability.

DISCUSSION

In spite of the morphological similarity and overlap between alpine populations of *Cerastium arvense* and *C. beeringianum*, the two taxa were separable on the basis of characters used in this study. This was especially true of garden specimens (see Fig. 4). As predicted from taxonomic treatments (Fernald and Wiegand 1920, Hultén 1956, Hitchcock et al. 1964), vegetative characters were more useful in distinguishing the taxa than were the conservative floral

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FIGS. 3–5. Principal components ordinations. 3. Forty field specimens from four populations: 1 = Deception Pass, 2 = Sumas Mountain, 3 = Twin Sisters, 4 = Chowder Ridge. 4. Forty garden specimens originally from four populations: 5 = Deception Pass, 6 = Sumas Mountain, 7 = Twin Sisters, 8 = Chowder Ridge. 5. Eighty field and garden specimens (populations numbered as above); populations 5, 6, 8 = *Cerastium arvense*, 7 = *C. beeringianum*.

characters. In general, bracts subtending the inflorescence were reduced and scarious-margined in *C. arvense*, foliaceous and non-scarious in *C. beerlingianum*. Leaves were narrower and longer in *C. arvense*, and axillary fascicles were restricted to the lower leaf nodes in *C. beerlingianum*. However, the separation of the taxa by principal components analyses was the result of the correlation of characters and not absolute differences between the taxa, thus the difficulty of field identification of alpine forms, as noted by Hitchcock et al. (1964).

The PCA's suggest that there is little genetic distinction between the alpine (Chowder Ridge) population and low elevation populations of *C. arvense*. However, the dwarf, mat-like growth habit of the former was apparently genetically fixed. In this respect the Chowder Ridge and Twin Sisters populations were similar. The two alpine populations also exhibited more variability in terms of seed germination requirements, a common adaptive characteristic of alpine plants. Flowering times were not similarly fixed since all populations flowered simultaneously in the garden. The large amount of phenotypic plasticity in non-serpentine populations is undoubtedly adaptive and helps to explain the broad ecological tolerance of *Cerastium arvense*. It also masks genetic distinctions among populations and species. This can be seen by comparing Figs. 3 and 4; the two species were much more distinct when grown under similar conditions. The restricted plasticity of the Twin Sisters and Sumas Mountain populations was perhaps due to selective pressures and specialization associated with the peculiarities of serpentine soils. Specialization is reflected not only by low plasticity, but also by the lower rooting success in non-serpentine substrates. Similar observations were recorded by Kruckeberg (1967) in his work with serpentine plants.

As previously noted, one of the objectives of this study was to confirm the taxonomic distinction of *Cerastium arvense* and *C. beerlingianum*. The selection of the Twin Sisters population was made for two reasons: it was a representative alpine population, and it was suspected to be *C. beerlingianum*. As noted above, this population was morphologically distinguishable, especially under uniform (garden) conditions (Fig. 4) and it proved to be tetraploid in contrast with the diploid *C. arvense* populations (Wagstaff 1986). Our study confirms, however, that because of phenotypic plasticity, the taxa cannot easily be distinguished in the field. From our limited study, it would seem that the keys and descriptions of Hitchcock et al. (1964) and Hultén (1956) are satisfactory but that the non-plastic and correlated characters, plant height, width of scarious margins of bracts, leaf width, and number of sterile shoots, should be emphasized.

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NOTEWORTHY COLLECTIONS

ARIZONA

AQUILEGIA TRITERNATA Payson \times *A. CHRYSANTHA* A. Gray (RANUNCULACEAE).—Coconino Co., Mogollon Rim, Dane Spring Canyon, at the base of a damp, shaded, sandstone cliff face, T13N R11E S35, 7 Jul 1987, *Schaack 2115 and Goodwin* (ASC).

Significance. The first known report of natural hybridization between *A. chrysantha* [*A. caerulea* group] with erect, yellow, long spurred [(40–)45–70 mm] flowers and *A. triternata* [*A. canadensis* group] with nodding, primarily red, short spurred [(12–)16–22 mm] flowers. Miller (Southw. Naturalist 30(1):69–76, 1985) did not see evidence of this hybridization during his research in the mountains of southern Arizona and indicated that the degree of genetic isolation between these species, due to habitat and pollination system, has not been studied. Flowers of the vouchered hybrid were intermediate in flower coloration (a curious mix of red and yellow) and spur length (32–35 mm). Hybrid flowers drooped on their peduncle ends. Two putative F_1 hybrids were the only hybridization products noticed at this site. The vouchered hybrid was rooted 0.46 m above ground level in a recess on a sheer, shaded, damp sandstone cliff face that housed the red flowered parent, *A. triternata*, above. The other hybrid was discovered growing in the understory, at streamside, among *A. chrysantha* just down canyon from the cliff face that held *A. triternata*. Although apparently a new *Aquilegia* hybridization report, this is but one in a series of known hybridizations, either artificial [Cockerell, Bot. Gaz. (Crawfordsville) 62:413–414, 1916; Anderson and Schafer, Ann. Bot. (London) 45:639–646, 1931; and Taylor, Brittonia 19:374–390, 1967] or natural (Grant, Aliso 2:341–360, 1952; and Miller, Amer. J. Bot. 65:406–414, 1978) between members of the *A. canadensis* and *A. caerulea* species groups. Seed was collected from the vouchered F_1 , later in 1987. Future research will include observation of pollinator activity between the parents and among parents and the putative reciprocal F_1 's and a search for the factors that apparently limit the establishment of backcross progeny at the Dane Spring Canyon population.—CLARK G. SCHAACK, Department of Botany, University of Wisconsin, Madison 53706 and GREGORY A. GOODWIN, Coconino National Forest, 2323 E. Greenlaw Lane, Flagstaff, AZ 86004.

STYLOCLINE SONORENSIS Wiggins (ASTERACEAE).—Representative collections: Graham Co.: Hawk Hollow, 26 Apr 1935, *Maguire s.n.* (ARIZ, det. as *Evax multicaulis* DC. or *Stylocline gnaphaloides* Nutt.; NY, mixed with and det. as *Filago californica* Nutt.). Pima Co.: Tucson, Desert Research Laboratory, sandy plain w. of Tumamoc Hill, 26 Apr 1968, *Turner 68-146 and Mason* (ARIZ, mixed with *Filago depressa* A. Gray; det. as *Stylocline micropoides* A. Gray); mesas near Camp Lowell, 15 Apr 1881, *Pringle s.n.* (F, MICH, both mixed with *S. gnaphaloides* and *S. micropoides* and det. as the latter). Pinal Co.: Big Wash 0.5 mi [0.8 km] nw. of Oracle Junction on route 89, 29 Apr 1965, *Hermann 19770* (RM, det. as *S. micropoides*). Santa Cruz Co.: ca. 16 mi [26 km] n. of Nogales along Hwy. 89, 27 Mar 1970, *Higgins 2813* (BRY, mixed with *Filago californica*; det. as *F. depressa* A. Gray). Also known from ca. 10 other collections in the above counties. Morefield thanks the curators of the herbaria above for loans of material in their care.

Previous knowledge. See CA Noteworthy Collections, below.

Significance. First reports for the United States.—JAMES D. MOREFIELD, see note below.

CALIFORNIA

STYLOCLINE SONORENSIS Wiggins (ASTERACEAE).—Riverside Co.: Hayfields, n. of Chuckwalla Mts., Colorado Desert, 2 Apr 1930, *M. E. Jones 25845* (POM, originally determined as *Evax multicaulis* DC., then as *S. micropoides* A. Gray).

Previous knowledge. Based only on the holotype (Mexico, n. Sonora, "One mile north of Cumeral, on road to Nogales", 9 Apr 1932, *Abrams 13199*, DSI) and on the original description (Contrib. Dudley Herb. 4:26, 1950).

Significance. First report for the United States. The species is an inconspicuous gray-woolly spring annual, and probably is more widespread in the Colorado Desert of CA than the single extant CA specimen would indicate. It should be considered rare and endangered in CA, however, until more sites can be located. The Hayfields population may well have been extirpated after 1930 by development activities. The species is more widespread in s. AZ (see AZ Noteworthy Collections, this issue).—JAMES D. MOREFIELD, Rancho Santa Ana Botanic Garden, 1500 N. College Ave., Claremont, CA 91711-3101.

ASPIDOTIS Densa (Brackenr. in Wilkes) Lellinger (SINOPTERIDACEAE).—San Diego Co., Cuyamaca Rancho State Park (CRSP), n. slope of Cherry Flat near Conejos Hiking Trail, 32°57'34"N, 116°36'35"W, 1800 m, moist rocky areas in gabbro outcrops, 8 Jul 1987, *Hirshberg s.n.* (SD).

Significance. A range extension of ca. 350 km s. from the Greenhorn Mts., Kern Co. Known previously from BC, Canada, s. to San Luis Obispo and Kern cos., CA, e. to ID, MT, and UT, always on serpentine-derived soils (Smith, Madroño 23:15, 1974; Lellinger, Field Manual of Ferns and Fern-Allies of U.S. and Canada, p. 149, 1985). Gabbro is an ultramafic rock chemically similar to serpentine.

HOLODISCUS BOURSIERI (Carrière) Rehder in Bailey (ROSACEAE).—San Diego Co., CRSP, n. side of Cuyamaca Peak on rocky cliff above Cherry Flat, 32°56'49"N, 116°36'22"W, 1920 m, 28 Jul 1987, *Hirshberg s.n.* (SD, UC) (det. R. Lis).

Significance. A range extension of ca. 115 km se. from the Santa Ana Mts., Orange Co., CA. Known previously from Trinity Co. s. to Orange Co., CA, and e. to w. NV. This genus is currently under revision and species determination is necessarily tentative (R. Lis pers. comm.).—JERILYN HIRSHBERG, P.O. Box 2, Julian, CA 92036 and GEOFFREY A. LEVIN, see note below.

ASTRAGALUS PACHYPUS E. Greene var. PACHYPUS (FABACEAE).—San Diego Co., Anza-Borrego Desert State Park, Bighorn Cyn., T13S R6E n.½ S2, 730 m, 14 Feb 1987, *A. Morley s.n.* (SD); same, 26 Feb 1987, *Morley s.n.* (SD) (det. R. C. Barneby). Few plants in sandy wash.

Significance. A range extension of ca. 250 km se. from Antelope Valley, Los Angeles Co. Known previously from Santa Barbara and Kern cos. se. to Los Angeles Co., and in San Benito Co.—GEOFFREY A. LEVIN, Botany Department, San Diego Natural History Museum, P.O. Box 1390, San Diego, CA 92112.

CARLOWRIGHTIA ARIZONICA A. Gray (ACANTHACEAE).—San Diego Co.: Anza Borrego Desert State Park, Borrego Palm Canyon Nature Trail ca. 2 km nw. of Borrego Springs, rocky slope in Sonoran desert scrub with *Larrea*, *Fouquieria*, *Justicia*, *Hyptis*, and *Encelia*, Borrego Palm Canyon 7.5' ser. T10S R5E S26 se.¼, ca. 300 m, 27 Mar 1988, *M. Bourell 3509* (CAS).

Previous knowledge. Northwestern Baja California, central Arizona, and west Texas southward throughout dry regions of Mexico, Honduras, and Nicaragua to northwestern Costa Rica (Guanacaste).

Significance. First report for this genus in California, doubling the number of taxa

of Acanthaceae in the state. Range extension of 220 km nw. of the nearest Mexican locality (Baja California, 9.5 km s. of La Ventana, *Daniel 1545*, ASU, CAS) and 230 km w. of the nearest known locality in the United States (Arizona, Yuma Co.: Kofa Mountains, various collectons cited in Daniel, *Fl. Neotrop.* 34:1–116, 1983). The California population marks the western limit of the distribution of both species and genus. Of the numerous forms discussed by Daniel (*ibid.* and *Desert Pl.* 5:162–179, 1984) in this morphologically diverse species, *Bourell 3509* most closely resembles plants originally described as *C. californica* var. *pallida* I. M. Johnst. from Baja California, indicating a link with plants from that region rather than with those from Arizona. —MONA BOURELL and THOMAS F. DANIEL, Department of Botany, California Academy of Sciences, Golden Gate Park, San Francisco 94118.

BAJA CALIFORNIA SUR

QUERCUS OBLONGIFOLIA Torr. (FAGACEAE). —Mpio. de La Paz, Sierra de la Victoria, oak woodland community, road to San Antonio de la Sierra Ranch, 6 km se. of El Triunfo, 900 m, 23°43'N, 110°03'W; small population; *José L. León 1132* (CIB). Additional trees have been seen in exposed sites at middle elevations in the Sierra de la Laguna, where they are called “encino laurel”. (Det. by comparison with specimens at CAS.)

Significance. A range extension of 420 km se. from the Sierra de la Giganta where it was reported by Carter (1955; “Observaciones sobre los encinos de Baja California”, *Bol. Soc. Bot. Mex.* 18:39–42).

QUERCUS ARIZONICA Sargent (FAGACEAE). —Mpio. de La Paz, Sierra de la Laguna, oak-pine woodland community, 2 km n. of La Laguna meadow, 1790 m, 23°36'N, 109°58'W, *José L. León 1887, 2331* (CIB). A unique population of about 50 trees. Acorn production is uncertain in this area. (Det. by D. E. Breedlove.)

Significance. Known previously in mountains of Arizona, and in the Sierra Madre Occidental of Sonora and Chihuahua. Near the collection site is a deep brook where *Quercus reticulata* H. & B. grows; the main distribution of this species is also in the Sierra Madre Occidental. —JOSÉ LUIS LEÓN DE LA LUZ, Centro de Investigaciones Biológicas de Baja California Sur, Apdo. postal 128, La Paz, Baja California Sur, México.

REVIEW

Conservation and Management of Rare and Endangered Plants. Edited by THOMAS S. ELIAS. 630 pp. California Native Plant Society. Sacramento, CA. 1987. ISBN 0-943460-11-5 (cloth), \$45.00, ISBN 0-943460-12-3 (paper), \$24.95.

This significant volume is the proceedings of a well-attended conference on rare and endangered plants held under the auspices of the California Native Plant Society in November of 1986. The objective of the conference was to bring together persons interested in the biology, management, and preservation of rare plants for exchange of ideas and information. The editors also sought early publication of the proceedings, a goal which they achieved in good style. The resulting volume includes 92 papers by 106 authors. Both the picture and typography on the cover are very attractive—suitable for display on the coffee table. The back cover, somewhat less striking, provides a picture key for the identification of the editor and conference coordinator (J. R. Nelson).

Twenty papers addressed the social, legal, and institutional aspects of rare plant protection and management. Though not the most riveting part of the volume, they provide a valuable summary of the current laws and programs relevant to rare plant conservation. The articles by Bartel and Cochrane will probably be especially useful as references. About 15 papers deal with research needs and general methodology. Among the topics addressed are reserve design, methods for sampling rare plants, the role of artificial propagation, and computerized systems for storing and analyzing data on rare plant habitat. The remaining papers are mostly case studies, though many also attempt to generalize. Genetic and evolutionary questions are addressed in a number of papers (e.g., Ledig, Conkle, Palmer), but the primary emphasis is on population and community ecology. The work reported ranges from sophisticated long-term studies (e.g., Kruckeberg on serpentine, Palmer's study of *Holocarpha*) to brief reports on obviously still-incomplete work in progress. The papers mostly deal with California though Arizona work is reported in three papers and other studies describe situations in Oregon, New Mexico, Alberta, Minnesota, and South Africa.

Though the editor and conference organizers are to be commended for getting the volume out promptly, this no doubt contributed to the major problem with the book—the uneven quality of the contributions. A few papers have major typographical and stylistic blunders that more leisurely editing might have caught. Peer review would also have shortened and improved the papers, and justified the exclusion of some. Summary papers prepared after the conference that integrated the contributions and guided the reader through them would also have been valuable.

A curious sidelight, of uncertain significance, is the greater than random frequency of occurrence of some authors. One author appears on five papers (only four of which are listed in the General Index), two are involved in three papers, and nine others appear on two papers. Is this evidence that rare plant biologists, like some rare plants, are highly aggregated and have a tendency to inbreeding?

The heterogeneity of the contributions makes it difficult to summarize the major conclusions. It is apparent, as Messick and others point out, that we need more status data on population sizes, locations, and degree of protection and threat. We also need more information on the population ecology and life histories of rare plants, especially as these are affected by events of low frequency like fire and severe drought. The papers, as is appropriate for rare taxa, stress minimally intrusive observational methods. But experimental studies, where possible, are also necessary and should be supported by those agencies with the resources to do so.

The heterogeneity is also probably an accurate reflection of the diversity of persons and approaches that deal with rare plant problems. Research on rare plants is relatively new, geographically dispersed, and in large part low-tech and labor intensive. These circumstances favor decentralization and a release of variability. No doubt there will be evolution in the direction of greater uniformity as the most useful research methods and management techniques come to be recognized. This volume, by putting a large sample of the current activity before us, should speed the selection process. It provides a good review of the state of our knowledge about endangered plants. There is no doubt that these proceedings will have an influence on the direction that rare plant research will take in the future. It is a book anyone with an interest in rare plants, especially in California, will want to have.—PAUL H. ZEDLER, Department of Biology, San Diego State University, San Diego, CA 92182-0057.

ANNOUNCEMENT

CALIFORNIA BOTANICAL SOCIETY Schedule of Speakers 1988-1989

8:00 P.M. University of California, Berkeley LSB 2503*

<u>Date</u>	<u>Speaker and Topic</u>
15 Sep	Linda Newstrom Dept. Botany, University of California, Berkeley "Botany and ethnobotany of Chayote (<i>Sechium edule</i>)"
20 Oct	James Shevock U.S. Forest Service "Phytogeography of the southern Sierra Nevada"
17 Nov	John Thomas Dept. Biological Sciences, Stanford University "A history of botany in northern California"
19 Jan	Thomas Duncan, Christopher Meacham Dept. Botany, University of California, Berkeley "(1) Computerized image analysis and (2) Floristic data bases"
18 Feb	SPEAKER AND LOCATION FOR ANNUAL BANQUET TO BE ANNOUNCED
16 Mar	Roger Raiche University of California Botanical Garden, Berkeley "The native plant collection at the U.C. Botanical Garden"
20 Apr	Thomas Rosatti Jepson Herbarium, University of California, Berkeley "Systematics and ecology of <i>Arctostaphylos uva-ursi</i> in North America"
18 May*	Linda McMahan Center for Plant Conservation, Arnold Arboretum, Harvard University "Helping the Ark land: the role of botanical gardens in plant conservation" [joint meeting with the California Native Plant Society]

* Except 18 May, which will be at the U.C. Berkeley Botanical Garden

For a monthly reminder of the meetings, please notify Dr. James Affolter, Botanical Garden, University of California, Berkeley, CA 94720.

ANNOUNCEMENT

NEW PUBLICATION

KEELEY, J. E. 1988. *Bibliographies on chaparral and the fire ecology of other Mediterranean systems*, 2nd ed. California Water Resources Center, Univ. California, Rept. 69. 328 pp. ISSN 0575-4968 (paper-bound). [A series of lengthy bibliographies dealing with chaparral and other Mediterranean ecosystems, much expanded from 1st edition (1984). Bibliographies for (mostly California) chaparral are (1) evolution and systematics, (2) community structure, (3) fire and demography, (4) seed germination and allelopathy, (5) morphology and physiology, (6) soils and management, and (7) animals. Bibliographies are also included for (8) California grasslands and (9) California forests—fire and demography. For each Mediterranean system outside of California (Australia, Chile, Mediterranean Europe [including western Asia and northern Africa], and South Africa) there is a bibliography on fire and demography and a bibliography on morphology and physiology. Also included is a bibliography on fire and demography of miscellaneous (mostly non-Mediterranean) regions. English-language publications predominate. Because duplicate citations are not included under different headings, a search of more than one bibliography may be necessary to insure that all references on a particular topic are found.] Copies can be obtained from: Water Resources Center, University of California, Rubidoux Hall, Riverside, CA 92521; (714) 787-4327. The bibliographies can also be obtained for a nominal fee on IBM compatible floppy disks from Dr. Jon E. Keeley, Occidental College, Los Angeles, CA 90041.

ANNOUNCEMENT

SYMPOSIUM ON CALIFORNIA'S OAK WOODLANDS: ATTITUDES AND RESPONSIBILITIES

The Range Management Advisory Committee to the California Board of Forestry, and the California Department of Forestry and Fire Protection are sponsoring a symposium on California's Oak Woodlands: Attitudes and Responsibilities, 22–24 January 1989, at the Red Lion Inn, 2001 Point West Way, Sacramento, CA. Landowners, policy makers, planners, resource managers, realtors, investors, development consultants, engineers, and citizens will discuss key issues and viable options for conserving oak woodlands and hardwood range. Panel discussions will include: (1) Hardwood rangelands as investment property: implications for the future of the resource; (2) Development and planning in oak woodlands: opportunities and constraints; (3) County-level planning for hardwood resources; (4) Oak woodland and hardwood rangeland residents: attitudes and objectives; (5) Effects of hardwood policy; and (6) Is multiple use management possible? A complete program with registration information can be obtained by contacting the Natural Resources Institute, Humboldt State University, Arcata, CA 95521; (707) 826-4172.

ANNOUNCEMENT

ASSOCIATION OF CALIFORNIA HERBARIA

The Association of California Herbaria met on 30 July 1988 and voted to adopt a set of bylaws and to officially incorporate as a non-profit organization. The Association is organized for the purposes of (1) promoting the development and use of California herbaria; (2) effecting cooperation among California herbaria; and (3) increasing the awareness of the value of these herbaria for (a) maintenance and management of botanical diversity, (b) research in taxonomy and evolution of plants, and (c) training and education concerning plant resources.

All public and privately owned herbaria and working collections in California are eligible for membership. Dues are based upon the size of the herbarium or collection as follows: <5000 specimens—\$5.00/year; between 5000 and 50,000 specimens—\$10.00/year; between 50,000 and 100,000 specimens—\$25.00/year; between 100,000 and 500,000 specimens—\$50.00/year; and >500,000 specimens—\$250.00/year. Each herbarium or working collection desiring to become a member of the Association should submit a request in writing to Dr. Thomas Duncan, Botany Department, University of California, Berkeley, CA 94720. Additional information and a request for payment of dues will be sent in reply.

SUBSCRIPTIONS—MEMBERSHIP

Membership in the California Botanical Society is open to individuals (\$22 per year; students \$12 per year for a maximum of seven years). Members of the Society receive MADROÑO free. Family memberships (\$25) include one five-page publishing allotment and one journal. Emeritus rates are available from the Corresponding Secretary. Institutional subscriptions to MADROÑO are available (\$30). Membership is based on a calendar year only. Applications for membership (including dues), orders for subscriptions, and renewal payments should be sent to the Treasurer. Requests and rates for back issues, changes of address, and undelivered copies of MADROÑO should be sent to the Corresponding Secretary.

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Presentation of nomenclatural matter (accepted names, synonyms, typification) should follow the format used for *Rhus integrifolia* in MADROÑO 22:288, 1974. Institutional abbreviations in specimen citations should follow Holmgren, Keuken, and Schofield, *Index Herbariorum*, 7th edition. Abbreviations of serial titles should be those in *Botanico-Periodicum-Huntianum* (Lawrence et al., 1968, Hunt Botanical Library, Pittsburgh). If the correct abbreviation cannot be determined, the full serial title should be used. Titles of books should be given in full, together with the place and date of publication, publisher, and edition, if other than the first.

All members of the California Botanical Society are allotted five free pages per volume in MADROÑO. Joint authors may split the full page number. Beyond that number of pages a required editorial fee of \$65.00 per page will be assessed. The purpose of this fee is not to pay directly for the costs of publishing any particular paper, but rather to allow the Society to continue publishing MADROÑO on a reasonable schedule, with equity among all members for access to its pages. Printer's fees for illustrations and typographically difficult material @ \$35.00 per page (if their sum exceeds 30 percent of the paper) and for author's changes after typesetting @ \$4.50 per line will be charged to authors.

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CALIFORNIA BOTANICAL SOCIETY

MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

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THE ROLE OF *CHRYSOLEPIS CHRYSOPHYLLA*
(FAGACEAE) IN THE *PSEUDOTSUGA*-HARDWOOD
FOREST OF THE KLAMATH MOUNTAINS
OF CALIFORNIA

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ABSTRACT

The tree form of *Chrysolepis chrysophylla* (giant chinquapin) is the most restricted and uncommon of the major sclerophyllous hardwoods in the *Pseudotsuga*-hardwood zone of the Klamath Mountains Geologic Province. The vegetation of three areas containing the species under different climatic conditions was examined to better understand its restriction. *Chrysolepis chrysophylla* was found to have the highest importance value of any hardwood tree averaged over all the sampling transects and was second in importance only to *Pseudotsuga menziesii*, the major canopy species. At all sites *C. chrysophylla* showed a distinct preference for mesic conditions with highest basal area cover occurring on northerly-facing slopes, or in mesic canyon bottoms. Seed-originated saplings were densest at the most mesic sites, whereas asexual sprouts were most prevalent at xeric sites. Areas of highest ground cover (>52%) appeared to have lower densities of sexual reproduction. *Lithocarpus densiflora* the predominant hardwood associate with *C. chrysophylla* had higher importance values at relatively low elevations, becoming insignificant at elevations above ca. 1000 m, whereas *C. chrysophylla* continued as an important forest component to above 1400 m. Comparative research from other areas in the Klamath Province indicate *C. chrysophylla* requires mesic northerly-facing exposures and an annual rainfall of 1524 mm or greater to attain subdominance. Its architecture pre-adapts it for subdominance of the highest, snowiest portions of the *Pseudotsuga*-hardwood zone at the interface with the *Abies concolor* zone. In contrast to previous assumptions, *C. chrysophylla* is a climax, as well as a successional species in its small zone of occurrence in the Klamath Mountains.

Giant chinquapin, *Chrysolepis chrysophylla* (Dougl.) Hjelmquist, is an evergreen sclerophyllous species that ranges from San Luis Obispo County in southwestern California to Madison County in west-central Washington. The main body of its distribution lies in the coastal areas of northern California and southern and central Oregon (Little 1971). Within this zone the species occurs in a variety of vegetation types ranging from mesic coastal forests dominated by western hemlock and redwood to montane mixed conifer, white fir, red fir, and chaparral associations (Franklin and Dyrness 1973, Taylor 1982, McKee ms.).

Whittaker (1960, 1961) lists giant chinquapin as one of the principal components of the mixed evergreen forest formation. Whittaker characterizes mixed evergreen forest as occurring in its most highly developed state in the Klamath Mountains Province and as the central prevailing climax for that area. According to Atzet and

Wheeler (1982, 1984) giant chinquapin occurs within the Douglas-fir, Port Orford cedar, and tanoak plant series in the Siskiyou Mountains, within the Klamath Mountains Province. These three series and the mixed evergreen forest of Whittaker are included within the broad classification known as the *Pseudotsuga*-hardwood forest of Sawyer et al. (1977). *Pseudotsuga*-hardwood forests occur in both the North Coast Range and Klamath Mountains provinces of California and adjacent Oregon.

The ecological role of *Chrysolepis chrysophylla* within the *Pseudotsuga*-hardwood zone is poorly understood. It is typically listed as one of the major hardwoods of the zone (Munz and Keck 1959, Sawyer et al. 1977, Holland 1986). However, it is not nearly as ubiquitous a species as the other principal sclerophylls; *Lithocarpus densiflora* (tanoak), *Quercus chrysolepis* (canyon live oak), or *Arbutus menziesii* (madrone). Only five out of ten candidate or established Forest Service Research Natural Areas within the Douglas-fir-hardwood zone of the Klamath province contain any significant giant chinquapin component, whereas seven contain tanoak and ten contain madrone and canyon live oak (Keeler-Wolf ms.). This restrictiveness is also indicated by the disjunct west slope Sierra Nevada distribution of the same broad-leaved sclerophyll species. Here giant chinquapin is the most restricted followed in order by tanoak, madrone, and canyon live oak (Griffin and Critchfield 1972).

Within a given area *Chrysolepis chrysophylla* is typically a species of lower crown cover than either madrone, canyon live oak, or tanoak. This point may be inferred from the maps of Griffin and Critchfield (1972), which rely in large part on the Vegetation Type Map and Soil-Vegetation surveys produced by the U.S. Forest Service. These surveys only list a tree species if it covers 20% or more (VTM) or 5% or more (S-V) of a given area. The areas of extensive stands of *Lithocarpus*, *Arbutus*, and *Quercus chrysolepis* shown in Griffin and Critchfield are much larger than those of *Chrysolepis*. Giant chinquapin's low density and cover is also indicated in Whittaker's extensive 1960 study of vegetation in the Siskiyou Mountains. There *C. chrysophylla* is in its greatest densities at elevations between 610 and 915 m on quartz diorite where it is between two and nine times less dense than the other sclerophylls. Whittaker's study indicates giant chinquapin is substantially reduced in density compared to most other evergreen sclerophylls on gabbro, and is only represented by an uncommon shrubby form on serpentine. In the Klamath Province the tree forms occupy mesic forest from near sea level to ca. 1600 m elevation, higher than any other broad-leaved sclerophyll except *Q. chrysolepis*.

The rather broad ecological amplitude of giant chinquapin alluded to in the first paragraph has much to do with the inclusion of shrubby ecotypes of *C. chrysophylla* (including *C. c.* var. *minor*, the golden

chinquapin) in the description of its range. These shrub forms may inhabit relatively xeric, poor soils, and/or high-elevation sites, and comprise most, if not all, of the individuals of the species south of Marin County, California (Whittaker 1960, Griffin and Critchfield 1972, Franklin and Dyrness 1973, McKee ms., D. Keil pers. comm.). The shrubby forms appear to be ecologically very different than the tree form. The tree form is usually restricted to mesic forest where it occurs as a subcanopy tree beneath a *Pseudotsuga*-dominated canopy.

Why should *Chrysolepis* be the least common of the major broad-leaved sclerophylls in the *Pseudotsuga*-hardwood forest? What conditions are optimum for growth of the species, and are these predictable, unifying conditions under which this species may form a major part of a community? I will attempt to answer these questions by investigating three different sites where giant chinquapin forms a significant part of the tree layer.

METHODS

The three sites selected for study are all in and adjacent to candidate and proposed Forest Service Research Areas (RNA's) in the Klamath Mountains Province of California (Fig. 1). All of these areas contain unlogged and otherwise humanly undisturbed examples of natural vegetation. The three sites contain principally mature or late successional forest with dominant canopy trees typically ranging in age from 250 to 600 years.

The Rough Gulch and Chinquapin Ridge proposed RNA's (referred to together as the Rough-Chinquapin site) lie adjacent to one another in southern Trinity County on the northern slopes of South Fork Mountain (ca. 40°15'N latitude, 123°15'W longitude). They include the most extensive study area (ca. 2500 ha) and range in elevation from ca. 800 to 1800 m. Slope aspects are primarily nne., although significant areas of e., n., and some w. and s. exposures also occur. The parent material is entirely South Fork Mountain Schist (Irwin 1966, 1981), an early Cretaceous metasediment prone to mass-wasting (Scott et al. 1980). Precipitation is estimated between 1524 and 1778 mm annually (Rantz 1972). This area was originally surveyed in 1984 (Keeler-Wolf 1984), but was re-visited and more thoroughly surveyed in 1987.

The second site occurs in and near the Bridge Creek RNA located in the southwestern Marble Mountains in western Siskiyou County (ca. 41°28'N latitude, 123°21'W longitude). This RNA covers ca. 730 ha, lies ca. 120 km north of the first site, and ranges in elevation from ca. 670 to 1280 m. It is underlain entirely by granitic rock of the Wooley Creek Pluton (Donato et al. 1982). Precipitation is estimated at between 1651 and 1778 mm annually (Rantz 1972). Slope

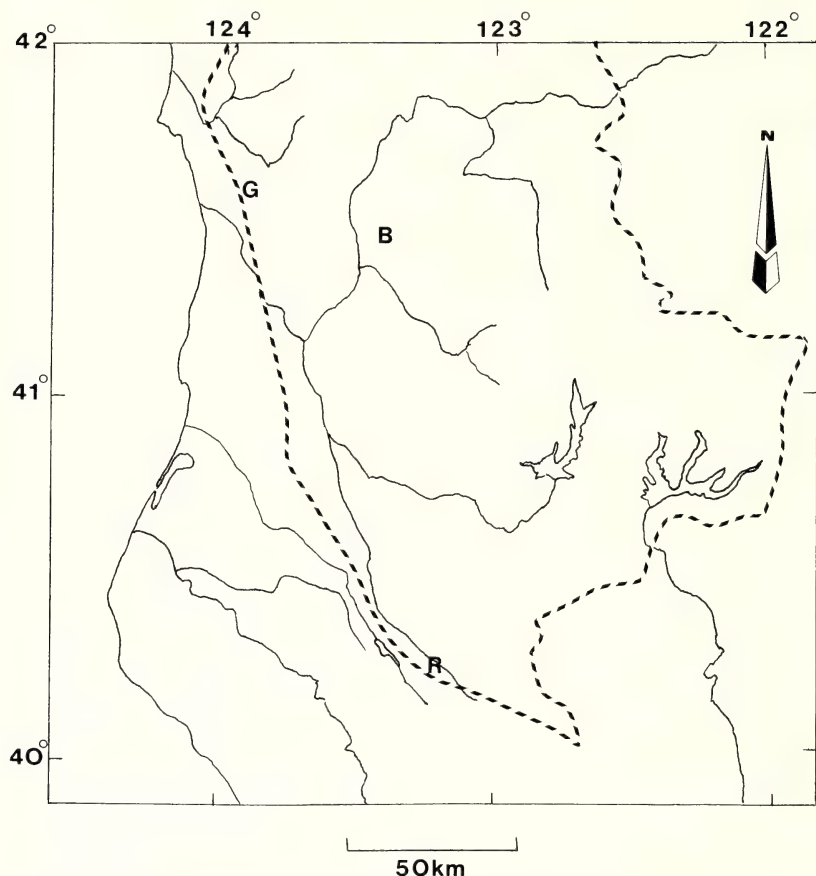


FIG. 1. Map of Northwestern California showing the boundary of the Klamath Province (dashed line) and the location of the three study sites; R = Rough-Chinquapin, B = Bridge Creek, and G = Goose Creek.

aspects are also varied, with all cardinal directions represented within the study area. Preliminary vegetation surveys were conducted in 1984 (Keeler-Wolf 1985) with additional work in 1987 both in and adjacent to the RNA.

The third site is centered within the Upper Goose Creek candidate RNA located in southern Del Norte County (ca. $41^{\circ}33'N$ latitude, $123^{\circ}52'W$ longitude). This site lies ca. 43 km nw. of Bridge Creek and is broken up into two units (total area of ca. 200 ha) that are separated by a small area of disturbed forest. Elevations at this site range from ca. 548 to 1097 m. The area is underlain by metasedimentary rocks of the Galice Formation (Irwin 1966). Precipitation is estimated at being between 2794 and 3048 mm annually (Rantz

1972). Slopes are predominantly north and south facing with smaller areas of west- and east-facing slopes. An ecological survey of the Upper Goose Creek candidate RNA was performed in 1986 (Keeler-Wolf 1987a) and additional work was conducted in 1987 both in the candidate RNA and in adjacent undisturbed forest on Lems Ridge.

Each area was first surveyed to determine major vegetation types, and coverage and distribution of giant chinquapin. Following this, representative stands of forest containing chinquapin were sampled using transects laid out along contours or compass bearings. Each transect was intended to represent a relatively homogeneous cover type, and an example of each type occurring at various slope exposures and aspects was sampled so that the broad spectrum of *Chrysolepis* occurrence in the area would be represented. Transects were terminated upon entering a visibly different vegetation type. The transects were punctuated every 50 or 75 m with a 10 × 10 m quadrat. In each quadrat the following information was obtained: 1) identity, density, and breast height cover of stems on all trees over 2 m, 2) density and identity of all tree saplings between 0.3 and 2 m in height, 3) density and identity of all seedlings of trees under 0.3 m in height, 4) presence and estimated percent cover of all shrub and herb species, 5) average slope aspect, 6) average elevation, and 7) average slope steepness. In this way 197 quadrats (ca. 2 ha) were sampled at the three sites. Chinquapin saplings were further broken down into sexual (seed-originated) and asexual (resprouts from stumps and trunk bases).

RESULTS

Forest composition. Table 1 shows importance values (relative density, relative frequency, and relative basal area cover summed and multiplied by 100) of all trees for all 11 transects. The mean value of these over the three sites indicates forests with highest importance values for *Pseudotsuga* with *Abies concolor* and *Chrysolepis* as the principal associated species. Of the 19 species of trees encountered, only these three had mean importance values over 16 and frequencies greater than 64%. However, eight additional species occur on 46% or more of the transects.

Table 2 indicates similarity values (Bray and Curtis 1957) based on importance values of trees for all stands on the three sites. The similarity values are generally high (\bar{x} = 0.642; where 0 = no similarity and 1 = total similarity) and indicate the relatively uniform frequency, density and cover of the major tree species. Note that similarity values varied within and between the three sites so that there were at least some pairs that had lower values within the same sites than between the three sites. The distribution of species at the

TABLE 1. MEAN IMPORTANCE VALUES FOR TREES OVER 2 M ON 11 TRANSECTS AT THE THREE SITES^a IN THE KLAMATH MOUNTAINS OF CALIFORNIA. ^aThe first letter in the transect name indicates the site; R = Rough-Chinquapin, B = Bridge Cr., G = Goose Cr.

	No. plots:											GU	Freq.	x I.V.
	RCN	RCR	RRN	REM	RUN	BLV	BMN	BLN	BUS	GM	GU			
	21	23	9	24	15	29	13	10	6	20	20			
<i>Pseudotsuga menziesii</i>	145.4	85.5	101.0	113.2	70.1	113.7	89.7	110.0	55.1	114.2	156.9	1.00	1.00	105.0
<i>Chrysopsis chrysophylla</i>	84.9	40.3	81.3	23.6	34.8	54.6	56.9	76.4	95.9	68.1	90.9	1.00	1.00	64.4
<i>Abies concolor</i>	37.1	109.6	75.3	84.3	132.0	72.8	43.6	65.2	58.3	—	—	—	0.82	61.7
<i>Lithocarpus densiflora</i>	—	—	—	—	—	8.3	43.8	—	6.1	76.7	36.9	0.46	0.46	15.6
<i>Pinus lambertiana</i>	20.5	36.4	24.9	11.4	46.3	6.4	17.9	—	—	—	—	—	0.64	14.9
<i>Pinus ponderosa</i>	—	18.5	6.5	11.8	12.8	—	—	—	24.0	—	—	—	0.46	6.7
<i>Taxus brevifolia</i>	2.5	—	—	3.1	—	7.2	13.8	45.1	—	—	—	—	0.46	6.6
<i>Arbutus menziesii</i>	3.1	4.3	4.4	2.0	—	4.4	—	—	26.8	—	8.5	0.64	0.64	4.9
<i>Cornus nuttallii</i>	4.0	—	3.7	8.1	4.0	14.9	11.3	—	—	3.9	—	0.64	0.64	4.5
<i>Quercus kelloggii</i>	—	11.9	—	10.9	—	—	—	—	22.9	—	—	0.27	0.27	4.2
<i>Acer circinatum</i>	—	—	—	—	—	13.1	11.5	—	—	16.3	—	0.27	0.27	3.7
<i>Calocedrus decurrens</i>	—	—	—	17.4	—	2.5	11.9	—	6.6	—	—	0.36	0.36	3.5
<i>Quercus chrysolepis</i>	2.7	—	—	1.5	—	1.3	—	3.2	8.9	13.7	—	0.55	0.55	2.9
<i>Acer macrophyllum</i>	—	—	—	10.7	—	1.1	—	—	—	—	—	0.18	0.18	1.1
<i>Tsuga heterophylla</i>	—	—	—	—	—	—	—	—	—	5.0	3.6	0.18	0.18	0.8
<i>Pinus attenuata</i>	—	—	—	—	—	—	—	—	—	—	3.3	0.09	0.09	0.3
<i>Chamaecyparis lawsoniana</i>	—	—	—	—	—	—	—	—	—	2.4	—	0.09	0.09	0.2
<i>Alnus rhombifolia</i>	—	—	—	1.7	—	—	—	—	—	—	—	0.09	0.09	0.2
<i>Salix scouleriana</i>	—	—	—	—	—	1.1	—	—	—	—	—	0.09	0.09	0.1

TABLE 2. SIMILARITY MATRIX BASED ON IMPORTANCE VALUES OF TREES ON 11 TRANSECTS AT THE THREE SITES IN THE KLAMATH MOUNTAINS OF CALIFORNIA.

	RCN	RCR	RRN	REM	RUN	BLV	BMN	BLN	BUS	GM
RCR	0.662									
RRN	0.822	0.789								
REM	0.653	0.765	0.745							
RUN	0.555	0.879	0.718	0.824						
BLV	0.742	0.698	0.810	0.780	0.627					
BMN	0.694	0.624	0.706	0.638	0.568	0.784				
BLN	0.762	0.637	0.809	0.678	0.567	0.794	0.680			
BUS	0.610	0.613	0.670	0.551	0.522	0.588	0.561	0.618		
GM	0.630	0.419	0.564	0.474	0.363	0.650	0.686	0.604	0.461	
GU	0.778	0.434	0.622	0.463	0.350	0.603	0.612	0.621	0.535	0.743

three sites indicates the Rough-Chinquapin area as being the most xeric inland location, lacking *Lithocarpus* and *Acer circinatum*, as well as the mesic coastal species such as *Tsuga heterophylla* and *Chamaecyparis lawsoniana*, which are restricted to the Goose Creek site.

Evidence for a moisture gradient from the Rough-Chinquapin to the Goose Creek sites is further indicated in the understory (shrub and herb) importance values (relative frequency summed with relative cover, multiplied by 100) on the sites (Table 3). Although a core of shrubs and herbs including *Chimaphila umbellata*, *Berberis nervosa*, *Vaccinium parvifolium*, *Rubus ursinus*, *Chimaphila menziesii*, *Pteridium aquilinum*, *Iris* spp., *Goodyera oblongifolia*, and *Viola sempervirens* occur regularly within all sites, several xeromorphic species such as *Arctostaphylos nevadensis*, *Ceanothus cordulatus*, *Quercus vaccinifolia*, and *Galium bolanderi* occur only at the most inland and xeric Rough-Chinquapin sites. Conversely, several mesomorphic species such as *Vaccinium ovatum*, *Gaultheria shallon*, *Coptis lacinata*, and *Blechnum spicant* occur only at the most mesic and coastal Goose Creek site. The largest number of species (58) occur at the Bridge Creek site, which is intermediate in moisture relations between the other two sites.

Similarity values (Table 4) between the importance values of shrub and herbaceous species on all transects are relatively low ($\bar{x} = 0.286$), but show the greatest dissimilarity between the Goose Creek and other sites. This is largely because of the high importance values of species unique, or nearly so, to that sample area such as *Vaccinium ovatum*, *Gaultheria shallon*, and *Rhododendron macrophyllum*. The similarity values between the Rough-Chinquapin and the Bridge Creek transects tend to be higher and there are only a few species that are not shared between the two areas. The slightly more mesic conditions at Bridge Creek are indicated best by the presence of *Quercus sadleriana* and *Achlys triphylla*, as well as by the relatively

TABLE 3. MEAN PERCENT COVER, FREQUENCIES, AND MEAN IMPORTANCE VALUES FOR SHRUBS AND HERBS ON 11 TRANSECTS AT THE THREE STUDY SITES IN THE KLAMATH MOUNTAINS OF CALIFORNIA. ^aPresence only at this transect indicated by x.

Species	\bar{x} % cover:	RCN	RCR	RRN	REM	RUN	BMN	BLN	BUS	BLV ^a	GM	GU	Freq.	x I.V.
Shrubs														
<i>Berberis nervosa</i>	14.4	—	—	6.9	45.9	2.5	18.5	29.2	—	x	16.1	6.8	0.82	14.0
<i>Gaultheria shallon</i>	—	—	—	—	—	—	—	—	—	—	53.3	63.1	0.18	11.6
<i>Corylus cornuta</i>	0.5	2.0	—	—	19.2	—	—	3.4	88.2	x	—	—	0.55	11.3
<i>Rhododendron macrophyllum</i>	—	—	—	—	—	—	6.7	—	—	—	46.0	44.9	0.27	9.8
<i>Quercus sadleriana</i>	—	—	—	—	—	—	17.6	29.8	24.7	x	—	18.1	0.46	9.0
<i>Vaccinium parvifolium</i>	11.2	—	—	23.1	3.1	6.5	15.8	12.0	—	x	3.2	—	0.73	7.5
<i>Gaultheria ovatifolia</i>	1.2	—	—	22.6	—	15.8	13.0	21.4	—	x	—	—	0.55	7.4
<i>Arctostaphylos nevadensis</i>	—	39.2	—	2.1	—	—	24.5	—	—	—	—	—	0.27	6.6
<i>Vaccinium ovatum</i>	—	—	—	—	—	—	—	—	—	—	56.1	—	0.09	5.6
<i>Rosa gymnocarpa</i>	6.0	—	—	—	7.4	—	8.2	2.0	—	x	—	—	0.46	2.4
<i>Rubus ursinus</i>	2.5	6.7	—	—	3.4	—	—	3.0	—	x	—	1.6	0.55	1.7
<i>Paxistima myrsinites</i>	—	—	—	—	—	—	2.6	10.2	—	x	—	—	0.27	1.3
<i>Symphoricarpos</i> spp.	1.5	—	—	—	6.8	—	—	—	—	x	—	—	0.27	0.8
<i>Vaccinium membraenaceum</i>	—	—	—	—	—	6.5	1.0	—	—	—	—	—	0.18	0.8
<i>Quercus vaccinifolia</i>	—	—	—	—	—	5.3	—	—	—	—	—	—	0.09	0.5
<i>Ceanothus cordulatus</i>	—	1.8	—	—	3.0	—	—	—	—	—	—	—	0.18	0.5
<i>Ceanothus prostratus</i>	—	—	2.1	—	—	—	—	—	—	—	—	—	0.09	0.2
<i>Rubus parviflorus</i>	0.5	—	—	—	—	—	—	—	—	x	—	—	0.18	0.1
<i>Amelanchier pallida</i>	0.5	—	—	—	—	—	—	—	—	x	—	—	0.18	0.1
<i>Rhamnus purshiana</i>	0.5	—	—	—	—	—	—	—	—	—	—	—	0.09	0.1
<i>Prunus emarginata</i>	—	—	—	—	0.8	—	—	—	—	—	—	—	0.09	0.1
<i>Toxicodendron diversiloba</i>	—	—	—	—	—	—	—	—	—	—	1.1	—	0.09	0.1
<i>Rhododendron occidentale</i>	—	—	—	—	—	—	—	—	—	x	—	—	0.09	—
<i>Cornus stolonifera</i>	—	—	—	—	—	—	—	—	—	x	—	—	0.09	—
<i>Euonymus occidentalis</i>	—	—	—	—	—	—	—	—	—	x	—	—	0.09	—
<i>Sambucus caerulea</i>	—	—	—	—	—	—	—	—	—	x	—	—	0.09	—

TABLE 3. CONTINUED.

Species	\bar{x} % cover:	RCN	RCR	RRN	REM	RUN	BMN	BLN	BUS	BLV ^a	GM	GU	Freq.	x I.V.
<i>Ribes roezlii</i>	—	—	—	—	—	—	—	—	—	x	—	—	0.09	—
<i>Salix</i> sp.	—	—	—	—	—	—	—	—	—	x	—	—	0.09	—
Herbs														
<i>Chimaphila umbellata</i>	24.9	102.2	24.2	4.6	24.3	37.9	29.8	50.0	—	x	—	10.6	0.91	30.8
<i>Xerophyllum tenax</i>	55.0	12.4	79.5	—	75.3	—	—	—	—	—	7.2	30.1	0.55	30.0
<i>Linnæa borealis</i>	22.4	—	12.7	11.4	1.3	12.7	23.2	—	—	x	—	—	0.64	8.4
<i>Pyrola picta</i>	5.5	10.2	4.2	4.1	10.7	5.6	6.9	—	—	x	—	—	0.73	4.7
<i>Iris</i> sp.	4.5	11.9	—	9.4	1.3	1.8	—	12.5	—	x	2.0	—	0.73	4.3
<i>Goodyera oblongifolia</i>	4.5	—	6.4	3.4	2.3	6.4	5.2	12.5	x	—	—	1.6	0.82	4.2
<i>Chimaphila menziesii</i>	1.0	1.6	4.2	1.6	4.8	4.0	1.0	12.5	—	—	3.1	7.4	0.91	4.1
<i>Whipplea modesta</i>	—	—	—	23.1	—	10.7	—	—	x	x	1.0	—	0.36	3.5
<i>Pteridium aquilinum</i>	6.3	3.9	—	11.0	1.3	—	1.0	—	—	x	—	11.7	0.64	3.5
<i>Achlys triphylla</i>	—	—	—	—	—	19.8	11.2	—	—	x	—	—	0.27	3.1
<i>Polystichum munitum</i>	1.0	—	—	11.2	1.3	1.0	—	—	—	x	6.4	—	0.55	2.1
<i>Disporum hookeri</i>	7.4	—	—	2.6	2.3	3.2	3.0	—	—	x	—	1.6	0.64	2.0
<i>Corallorhiza maculata</i>	1.0	6.7	—	4.9	1.3	0.8	2.0	—	—	x	—	0.8	0.73	1.8
<i>Viola sempervirens</i>	6.1	—	2.1	—	—	1.6	3.0	—	—	x	—	0.8	0.55	1.4
<i>Vancouveria hexandra</i>	2.5	—	—	1.6	—	2.6	1.0	—	—	x	—	—	0.46	0.8
<i>Bromus marginatus</i>	—	—	—	6.7	—	—	—	—	—	x	—	—	0.18	0.7
<i>Arnica discoides</i>	2.0	—	—	—	2.3	0.8	—	—	—	x	—	—	0.36	0.5
<i>Trientalis latifolia</i>	1.4	—	—	1.6	—	1.6	—	—	—	x	—	—	0.36	0.5
<i>Pterospora andromedea</i>	—	—	—	—	—	—	—	—	—	—	—	—	0.09	0.4
<i>Listera caurina</i>	3.9	—	—	—	—	—	—	—	—	—	—	—	0.09	0.4
<i>Festuca idahoensis</i>	—	1.6	—	1.6	—	—	1.0	—	—	—	—	—	0.27	0.4
<i>Elymus glaucus</i>	—	—	—	2.6	—	—	—	—	—	—	—	—	0.09	0.3
<i>Hieracium albiflorum</i>	1.5	—	—	1.6	—	—	—	—	—	x	—	—	0.27	0.3
<i>Viola glabella</i>	3.0	—	—	—	—	—	—	—	—	x	—	—	0.18	0.3
<i>Lupinus</i> sp.	—	—	2.1	—	—	0.8	—	—	—	—	—	—	0.18	0.3
<i>Pyrola secunda</i>	—	—	2.1	—	1.3	—	—	—	—	x	—	—	0.27	0.3

TABLE 3. CONTINUED.

Species	\bar{x} % cover:	RCN	RCR	RRN	REM	RUN	BMN	BLN	BUS	BLV ^a	GM	GU	Freq.	x I.V.
	26.9	23.0	71.8	28.9	40.3	32.8	51.8	5.5	—	—	79.2	83.3		
<i>Clintonia uniflora</i>	—	—	—	—	2.3	—	—	—	—	x	—	—	0.18	0.2
<i>Veratrum viride</i>	—	—	2.1	—	—	—	—	—	—	—	—	—	0.09	0.2
<i>Lilium washingtonianum</i>	0.5	—	—	—	1.3	—	—	—	—	x	—	—	0.27	0.2
<i>Galium triflorum</i>	—	—	—	1.6	—	—	—	—	—	x	—	—	0.18	0.2
<i>Coptis laciniata</i>	—	—	—	—	—	—	—	—	—	—	2.0	—	0.09	0.2
<i>Smilacina racemosa</i>	1.0	—	—	—	—	0.8	—	—	—	x	—	—	0.18	0.2
<i>Adenocaulon bicolor</i>	1.0	—	—	—	—	—	—	—	—	x	—	—	0.18	0.1
<i>Heuchera micrantha</i>	—	—	—	—	1.3	—	—	—	—	—	—	—	0.09	0.1
<i>Pyrola asarifolia</i>	—	—	—	—	—	—	—	—	—	x	—	0.8	0.18	0.1
<i>Monotropa hypopitys</i>	—	—	—	—	1.3	—	—	—	—	—	—	—	0.09	0.1
<i>Pyrola picta aphylla</i>	0.5	—	—	—	—	—	—	—	—	—	—	—	0.09	0.1
<i>Vicia americana</i>	0.5	—	—	—	—	—	—	—	—	—	—	—	0.18	0.1
<i>Fragaria californica</i>	—	—	—	0.8	—	—	—	—	—	x	—	—	0.09	0.1
<i>Bromus laevipes</i>	—	—	—	—	—	0.8	—	—	—	—	—	—	0.09	0.1
<i>Campanula prenanthoides</i>	—	—	—	0.8	—	—	—	—	—	—	—	—	0.09	0.1
<i>Calypso bulbosa</i>	1.0	—	—	—	—	0.8	—	—	—	—	—	—	0.18	0.1
<i>Thelypteris nevadensis</i>	0.5	—	—	0.8	—	—	—	—	—	x	—	—	0.27	0.1
<i>Asarum hartwegii</i>	0.5	—	—	—	—	—	—	—	—	x	—	—	0.18	0.1
<i>Blechnum spicant</i>	—	—	—	—	—	—	—	—	—	—	1.0	—	0.09	0.1
<i>Lathyrus</i> sp.	—	—	—	0.8	—	—	—	—	—	—	—	—	0.09	0.1
<i>Corallorhiza striata</i>	—	—	—	0.8	—	—	—	—	—	—	—	—	0.18	0.1
<i>Galium bolanderi</i>	0.5	—	—	—	—	—	—	—	—	x	—	—	0.09	0.1
<i>Habenaria elegans</i>	0.5	—	—	—	—	0.8	—	—	—	—	—	—	0.18	0.1
<i>Arenaria macrophylla</i>	—	—	—	—	—	—	1.0	—	—	—	—	—	0.09	0.1
<i>Osmorhiza chilensis</i>	—	—	—	—	—	—	—	—	—	x	—	—	0.09	—
<i>Trillium ovatum</i>	—	—	—	—	—	—	—	—	—	x	—	—	0.09	—
<i>Rubus nivalis</i>	—	—	—	—	—	—	—	—	—	x	—	—	0.09	—
<i>Festuca occidentalis</i>	—	—	—	—	—	—	—	—	—	x	—	—	0.09	—
<i>Anemone quinquefolia</i>	—	—	—	—	—	—	—	—	—	x	—	—	0.09	—
<i>Apocynum pumilum</i>	—	—	—	—	—	—	—	—	—	x	—	—	0.09	—

TABLE 4. SIMILARITY MATRIX BASED ON IMPORTANCE VALUES OF SHRUBS AND HERBS ON 10 TRANSECTS ON THE THREE STUDY SITES IN THE KLAMATH MOUNTAINS OF CALIFORNIA.

	RCN	RCR	RRN	REM	RUN	BMN	BLN	BUS	GM
RCR	0.281								
RRN	0.615	0.223							
REM	0.362	0.187	0.176						
RUN	0.545	0.378	0.693	0.142					
BMN	0.486	0.239	0.448	0.371	0.321				
BLN	0.496	0.184	0.449	0.364	0.326	0.707			
BUS	0.173	0.320	0.174	0.191	0.164	0.339	0.321		
GM	0.152	0.062	0.102	0.151	0.093	0.165	0.102	0.026	
GU	0.299	0.155	0.218	0.148	0.267	0.253	0.220	0.189	0.575

unimportant species, *Paxistima myrsinites* and *Rhododendron macrophyllum*.

Tree regeneration. The importance values (relative density + relative frequency \times 100) of saplings on the 11 transects indicate that the principal saplings throughout the three study areas are *Pseudotsuga*, *Abies concolor*, *Lithocarpus*, *Chrysolepis* (including both sexual and resprout saplings), and *Pinus lambertiana* (Table 5). However, *A. concolor* does not occur at the Goose Creek site and *Lithocarpus* does not occur at the Rough-Chinquapin site. The data for seedlings (Table 6) indicate that *Pseudotsuga*, *A. concolor*, *Chrysolepis*, *Lithocarpus*, *Quercus chrysolepis*, and *Pinus lambertiana* are the most important species.

The combined importance values of both resprout and seed-originated saplings of *Chrysolepis* exceeds all other hardwood species at the Rough-Chinquapin sites (Table 5). However, *Lithocarpus* saplings may exceed total *Chrysolepis* saplings at both Bridge Creek (BMN and BUS) and at the Goose Creek site (GM).

When importance values of seed-originated saplings of giant chinquapin are compared with densities of basal or stump sprout-originated saplings it is clear that at the Rough-Chinquapin site asexual reproduction is prevalent. There, ratios of sexual to asexual saplings ranged from total asexual representation on transect REM to 0.731 at RCN with an average of 0.294 for the five transects. In contrast, both the Bridge Creek and the Goose Creek sites had ratios of sexual to asexual saplings all greater than 1.0. At Goose Creek these were 1.09 and 1.35 whereas at Bridge Creek these ranged from total sexual reproduction on BLE to 2.58 at BMN with an average of 8.06.

The densities of seedlings on the 11 transects were not lowest at the Rough-Chinquapin site. Seedling densities were consistently low at all sites, with the highest densities occurring at the RCN (16/ha⁻¹) and RUN (9/ha⁻¹) transects at the Rough-Chinquapin site. All other transects ranged between 0 and 3 seedlings per 0.1 ha.

TABLE 5. FREQUENCY AND MEAN IMPORTANCE VALUES FOR SAPLINGS (>0.3 m, <2 m) ON 11 TRANSECTS AT THREE STUDY SITES IN THE KLAMATH MOUNTAINS OF CALIFORNIA.

Species	RCN	RCR	RRN	REM	RUN	BLV	BMN	BLN	BUS	GM	GU	Freq.	\bar{x} I.V.
<i>Abies concolor</i>	41.3	110.4	74.1	95.3	114.3	69.4	30.4	59.9	38.2	—	—	0.82	57.6
<i>Pseudotsuga menziesii</i>	92.0	38.2	62.2	51.3	13.3	29.1	28.2	24.6	13.9	—	56.6	0.91	37.2
<i>Lithocarpus densiflora</i>	—	—	—	—	—	14.0	76.0	—	59.4	132.5	56.0	0.46	30.7
<i>Chrysolepis</i> (sex.)	7.9	2.4	4.6	—	15.6	40.4	31.7	63.7	—	28.8	43.5	0.82	21.7
<i>Chrysolepis</i> (sprt.)	10.8	25.3	26.7	3.9	33.1	2.3	12.3	15.8	24.3	21.3	39.9	1.00	19.6
<i>Pinus lambertiana</i>	37.4	23.9	20.5	20.4	20.0	2.4	—	3.4	—	—	—	0.64	11.6
<i>Quercus chrysolepis</i>	7.9	—	—	2.1	—	4.9	—	—	36.4	17.5	4.1	0.55	6.6
<i>Taxus brevifolia</i>	—	—	4.1	—	—	17.0	8.7	28.2	—	—	—	0.36	5.3
<i>Calocedrus decurrens</i>	—	—	—	14.4	—	6.1	—	—	13.9	—	—	0.27	3.1
<i>Cornus nuttallii</i>	2.8	—	4.1	10.5	3.6	7.0	3.8	—	—	—	—	0.55	2.9
<i>Arbutus menziesii</i>	—	—	4.1	—	—	6.5	3.0	—	13.9	—	—	0.36	2.5
<i>Acer circinatum</i>	—	—	—	—	—	—	5.9	4.5	—	—	—	0.18	1.0
<i>Pinus ponderosa</i>	—	—	—	2.1	—	—	—	—	—	—	—	0.09	0.2
<i>Salix scouleriana</i>	—	—	—	—	—	1.2	—	—	—	—	—	0.09	0.1

TABLE 6. FREQUENCY AND MEAN IMPORTANCE VALUES FOR SEEDLINGS (<0.3 m) ON 11 TRANSECTS AT THREE STUDY SITES IN THE KLAMATH MOUNTAINS OF CALIFORNIA.

Species	RCN	RCR	RRN	REM	RUN	BLV	BMN	BLN	BUS	GM	GU	Freq.	\bar{x} I.V.
<i>Pseudotsuga menziesii</i>	134.9	74.8	107.4	106.0	36.1	97.9	55.5	58.9	—	87.5	156.7	0.91	83.2
<i>Abies concolor</i>	8.6	92.8	72.8	54.9	116.5	63.9	49.6	98.4	—	—	—	0.73	50.7
<i>Chrysolepis chrysophylla</i>	34.9	18.7	13.2	9.4	28.7	4.8	23.4	—	—	37.5	21.0	0.82	17.4
<i>Lithocarpus densiflora</i>	—	—	—	—	—	8.0	51.5	—	53.2	37.5	22.4	0.46	15.7
<i>Quercus chrysolepis</i>	8.9	—	—	3.7	—	2.4	—	—	84.4	37.5	—	0.46	12.5
<i>Pinus lambertiana</i>	6.2	13.8	6.6	3.7	14.1	5.2	10.1	19.3	—	—	—	0.73	7.2
<i>Calocedrus decurrens</i>	—	—	—	9.3	—	2.4	10.1	—	31.2	—	—	0.36	4.8
<i>Quercus kelloggii</i>	3.2	—	—	13.1	4.7	—	—	—	31.2	—	—	0.36	4.8
<i>Taxus brevifolia</i>	—	—	—	—	—	13.1	—	23.9	—	—	—	0.18	3.4
<i>Cornus nuttallii</i>	3.2	—	—	—	—	2.4	—	—	—	—	—	0.18	0.5

TABLE 7. DENSITY AND BASAL AREA OF *Chrysolepis*, TOTAL BASAL AREA AND DENSITY OF ALL TREES, DENSITY OF SEXUAL AND ASEXUAL *Chrysolepis* REPRODUCTION, AND SLOPE DIRECTION AND ELEVATION OF ALL TRANSECTS AT THREE STUDY SITES IN THE KLAMATH MOUNTAINS OF CALIFORNIA. ^aDensity figures are per ha⁻¹. ^bCover figures are m²/ha⁻¹. ^cNot applicable due to inner valley location.

Transect	<i>Chrysolepis</i> density ^a	Total tree density	<i>Chrysolepis</i> sapling and seedling density (sexual)	<i>Chrysolepis</i> sprout density	<i>Chrysolepis</i> cover ^b	Total cover	\bar{x} slope direction	\bar{x} elev. (m)
RCN	42	118	19	4	2.44	13.90	n.	1020
RCR	16	179	4	19	2.31	15.80	nnw.	1390
RRN	37	147	4	26	4.16	12.70	n.	1180
REM	7	106	1	1	1.20	15.87	ene.	1220
RUN	11	126	9	27	0.59	11.01	n.	1432
BLV	54	175	49	3	0.76	16.33	— ^c	1158
BMN	27	154	20	5	1.94	10.94	nnw.	1036
BLN	62	156	70	8	1.45	13.89	n.	975
BUS	42	118	0	3	3.07	7.93	ssw.	1220
BLE	10	155	20	0	1.28	5.72	e.	1073
GM	28	110	3	3	1.98	11.51	nnw.	716
GU	36	90	23	12	1.28	9.42	n.	1082

Dominance and slope aspect. The total basal area cover (m²/ha⁻¹) for tree size chinquapin on all transects is shown in Table 7. The very highest cover is at RRN on a north-facing slope that averages ca. 1180 m elevation. The lowest cover is at RUN, which is an upper north-facing slope averaging ca. 1432 m elevation. When just the seven mid-slope transects (modal positions, as opposed to obviously mesic lower slope and xeric ridgetop locations) are considered, the highest cover consistently occurs on slope aspects which average between n. and nnw. The lowest cover in these seven modal transects occurs at REM, with an average slope aspect of ene. In a thorough survey of slope aspects at all three study sites no extensive modal slope areas were found where *Chrysolepis* occurred on aspects to the south of due e. or due w. This was true even at the wettest Goose Creek site. The only locations south of e. and w. where *Chrysolepis* formed a significant cover were in ravines and valley bottoms (e.g., BLV, BLE) or at summit ridges (RCR, BUS). Table 7 indicates that there is no correlation between total tree cover and chinquapin cover.

Moisture and reproduction. The highest densities of sexually reproducing giant chinquapin (saplings and seedlings combined) generally occur at the most mesic sites. These sites (BLV, BLN, see Table 7) are in valley bottoms, which, although not typically within



FIG. 2. Typical mesic north-facing understory exhibiting good *Chrysolepis* sexual regeneration. Rough-Chinquapin site ca. 200 m from South Fork of Trinity River, elevation 800 m.

the influence of permanent stream moisture, are at least experiencing the effects of the relatively cool, shady environment (equivalent to moisture gradient steps 1 and 2 of Whittaker 1960). Concomitantly, the areas with lowest densities of seed-generated reproduction occur on relatively xeric upper slopes (steps 6–8 of Whittaker 1960). These include RCR, RRN, REM, and BUS transects (Table 7). These xeric exposures are either near ridgetops (RCR and BUS) or are on relatively open upper slopes. This situation is the rule throughout the Bridge Creek and Rough-Chinquapin sites. Despite the fact that no lower slope sites were sampled at Rough-Chinquapin, observation (Fig. 2) indicates highest densities of sexual reproduction on the lowest, mesic slopes in that area. The only exception to this rule is at the Goose Creek site where the upper slope GU transect has higher densities of saplings and seedlings than the mid-slope GM site.

Ground cover and moisture relations. As can be seen from Table 3 the average percent ground cover ranges from a low of ca. 6 at the largely south-facing BUS ridgetop transect to a high of 83 at the upper slope Goose Creek site (GU). Although there is a trend toward increasing cover at wetter sites, this is confounded by the presence of high densities of *Xerophyllum tenax* (beargrass) at RRN and RUN, which otherwise have relatively xeric understories (its presence at these sites may relate to a history of slope instability). Al-



FIG. 3. Typical dense undergrowth of *Rhododendron macrophyllum*, *Vaccinium ovatum*, and *Gaultheria shallon* at the wet-coastal Goose Creek site.

though the most mesic lower slope sites at BLV and BLN were shown to have the highest densities of sexual reproduction, the effect of understory density on sexual reproduction of chinquapin is negative at high values (above ca. 52% cover). The five transects between 52 and 83% cover show a negative correlation ($r = -0.85$, d.f. = 3, $t = 3.09$, $p = 0.05$) with sexual sapling and seedling density. This suggests that the shade cast by high shrub and herb cover is inhibiting germination and/or growth of *Chrysolepis* seedlings (Fig. 3). Thus, chinquapin appears to reproduce best sexually in areas where mesic conditions prevail, but where conditions are not conducive to dense layers of understory species.

In contrast asexual reproduction by basal and stump sprouting appears to be more prevalent at relatively xeric sites. The highest values occur on the ridgetop and upper slope sites at Rough-Chinquapin.

Elevation and tree distribution. The importance of *Lithocarpus densiflora* in the forests at Bridge Creek and Goose Creek establish that it is the principal hardwood and subcanopy associate of *Chrysolepis*. When *Lithocarpus* and *Chrysolepis* importance values are compared at sites of co-occurrence, it appears that *Lithocarpus* is most important at the lowest elevation site (GM) and least important at the highest elevation sites (BLV, BUS). Elevation and importance of *Lithocarpus* are negatively correlated with increasing elevation ($r = -0.89$, $t = 3.38$, d.f. = 3, $p = 0.05$). On the other hand, *Chrysolepis*

dominance and importance within areas of *Lithocarpus* presence are not correlated with altitude (716–1220 m). However, if the area with the greatest altitudinal variation, Rough-Chinquapin, is analyzed there is a strong negative correlation between altitude and chinquapin importance on the four transects with similar slope exposure ($r = -0.99$, $t = 98.0$, d.f. = 2, $p > 0.001$). Importance values (I.V.) drop off sharply above 1200 m. Observation in higher elevation areas adjacent to the other two study areas containing *Lithocarpus* confirm that giant chinquapin cover drops at a much higher elevation than *Lithocarpus* cover.

DISCUSSION

Comparative data confirm requirements for Chrysolepis subdominance. A review of the other surveyed Forest Service candidate RNA's within the *Pseudotsuga*-hardwood zone of the Klamath Province reaffirms the data from this report and indicates the regular requirements of the species. Giant Chinquapin is unimportant or absent at the Adorni (Sawyer 1981), Ruth (Thornburgh 1981), Hennesy Ridge (Thornburgh 1987), Peach Creek (Keeler-Wolf 1987b), and Williams Point (Sawyer and Stillman 1977a) candidate RNA's and is present in relatively low density and cover at Specimen Creek (Sawyer and Stillman 1977b) and South Fork Mountain (Taylor 1975). What emerges is that *Chrysolepis* requires cool, mesic northerly-facing exposures and an annual rainfall regime of ca. 1524 mm or greater to attain subdominance in the *Pseudotsuga*-hardwood forest of Klamath Province.

Chrysolepis compared with Lithocarpus and other broad-leaved sclerophylls. *Chrysolepis* predominates on mesic northerly-facing slopes, where it co-dominates the subcanopy with *Lithocarpus* at lower elevations, but comes to dominate the subcanopy above ca. 1000 m elevation (or at lower elevations of sites inland from the distribution of *Lithocarpus*). Although *Lithocarpus* is tolerant of shade and high moisture (Roy 1957) *Chrysolepis* is apparently more tolerant of moisture. At the BLN site *Chrysolepis* was found at its greatest importance values with *Lithocarpus* totally lacking from the transect. This was surprising because *Lithocarpus* was common on surrounding adjacent higher elevation, more xeric and exposed slopes, suggesting that the shady, mesic BLN location with its high importance of *Taxus*, an indicator of very mesic conditions (Whittaker 1960, Atzet and Wheeler 1982), was too mesic to support *Lithocarpus* (Fig. 4). However, the relatively high I.V. of *Lithocarpus* saplings at the shady, high understory cover GM transect indicates that tanoak may be slightly more shade tolerant than *Chrysolepis* saplings.

In addition to its shade and moisture tolerance, *Chrysolepis* is



FIG. 4. Lower north slope *Pseudotsuga*—*Chrysolepis* forest with dense cover of *Chrysolepis* saplings and *Taxus brevifolia*, BLN site.

considerably more cold- and/or snow-tolerant than *Lithocarpus*, or *Arbutus*. This is supported in the data on elevational distribution and clearly indicated by the presence of tree-sized *Chrysolepis* on north-facing slopes up to 1600 m in elevation, whereas *Lithocarpus* and *Arbutus* both lose their tree form at ca. 1220 m. The architecture of both *Lithocarpus* and *Arbutus* is very different from *Chrysolepis* and provides a clue to their low densities or absence in the upper elevations of this zone. Both *Arbutus* and *Lithocarpus* have relatively broad, plane or concave leaves with typically ascending branches of mature trees. The outlines of uncrowded mature *Lithocarpus* and *Arbutus* tend to be relatively broad at the top and at best cylindrical. Conversely, *Chrysolepis* has typically longitudinally reflexed, convex leaves that are relatively narrow. In addition, mature trees of *Chrysolepis* typically have principal branches deflexed, and uncrowded mature trees tend to have a conical shape, similar to middle aged *Pseudotsuga* or *Abies concolor*. The net result is that the snow shedding abilities of the tree form of *C. chrysophylla* are superior to those of all other sclerophyllous hardwoods in California (Fig. 5). Although shrubby *Quercus chrysolepis* may occur at higher elevations (over 1800 m), these are always southerly exposures where snow tends not to accumulate and melts quickly. Thus, *Chrysolepis* appears to be pre-adapted as the predominant sclerophyll of the mesic upper elevations of the *Pseudotsuga*-hardwood zone.

Asexual versus sexual reproduction. The giant chinquapin has been



FIG. 5. A 17 m tall *Chrysolepis* at ca. 1550 m surrounded by *Abies concolor* forest. Snow depth ca. 45 cm, Rough Gulch, 13 November 1984.

considered a poor and irregular seeder (mast seeding reported at 2–5 year intervals) with resprouting its main mode of regeneration (Roof 1969, 1970, Atzet and Wheeler 1982, McDonald et al. 1983, McKee ms.). In fact, McDonald et al. (1983) report giant chinquapin as having the poorest germination rate of all hardwoods in the Klamath Province (14–53%). However, it is able to sexually establish itself under mesic conditions in shade or partial shade at all three of the sample areas in this report. Within the three sites it appears to require a more mesic seed-bed than does *Lithocarpus* and does not establish well from seed on upper slopes, ridges, or southerly exposures except perhaps during an abnormally moist series of years. The density of

seedlings in some areas without numerous saplings (e.g., RCN) suggests that the survivorship of seedlings at those sites is low. The site BLN indicates the affinity the species has for shady, mesic nursery conditions, suggesting that under more widespread mesic conditions in the Miocene (e.g., Axelrod 1977) it was a more common tree, more tolerant of extremely mesic conditions than *Lithocarpus*, which today appears to prefer summer fog or maritime influence, but is able to tolerate drier slope aspects. The widespread restriction to northerly-facing slopes is probably best explained by the long-lasting and year-round moisture requirements for seedling establishment.

Once established, however, giant chinquapin is able to tolerate relatively high moisture stress, evidenced by the presence of stands on ridgetops and upper slopes. Its drought tolerance as a mature tree and its ability to resprout vigorously have added greatly to its present day ecological amplitude.

Chrysolepis reproduces asexually by adventitious budding from stumps and basal burls after fires or other disturbance (e.g., wind and snow damage, logging, and browsing by herbivores). Transect BUS is a good example of a resprout xeric type which probably originated from seed dispersed from adjacent north slope stands long ago during a wet regime and is maintained through vigorous post-fire resprouting (the last fire at BUS was ca. 1936). Resprout stems averaged 2–3 per clump (with a maximum of 7) and ca. 28 cm dbh. The largest reprints were ca. 46 cm dbh and ca. 24 m tall. This contrasts sharply with typical seed-originated stems on n. slopes which average ca. 140 years for 46 cm dbh.

Longevity versus reproductive ability. Trees average more stems per ha on mesic sites, but the longest-living trees and the largest individuals occur at more xeric sites such as mid-slopes at Rough-Chinquapin. Ages of mature chinquapins are often difficult to obtain due to heart rot and indistinct annual rings. However, the few I successfully aged indicated specimens on north slopes grow relatively slowly and uniformly, attaining diameters of ca. 60 cm in ca. 210–260 years. The oldest *Chrysolepis* stems (those at Rough-Chinquapin ca. 122 cm dbh) had estimated ages of 400–500 years. The Bridge Creek and Goose Creek sites had fewer trees in the large size classes than Rough-Chinquapin, the largest measured there were ca. 81 cm dbh (Bridge, Fig. 6) and 70 cm dbh (Goose). Heart rot was more prevalent at Bridge and Goose creeks and may be the reason for fewer large trees at both sites. It appears, from the lack of young trees on many of the upper slope and xeric sites, that sexual reproduction there is sporadic with major bursts perhaps once every few hundred years. Yet, the more xeric conditions may be less conducive to fungal damage to heartwood, apparently the main cause of death in mature trees of undisturbed forest.



FIG. 6. One of the largest *Chrysolepis* individuals noted at the Bridge Creek study site (transect BMN). This tree (in center) is ca. 35 m in height with a dbh of 75 cm. *Pseudotsuga* to right is 86 cm dbh.

Successional versus climax species? Atzet and Wheeler (1982) and McKee (ms.) consider *C. chrysophylla* to be an early successional species only. However, contrary to these reports, giant chinquapin does not necessarily decline in importance in late stages of succession. For example, the Bridge Creek lower valley (BLV) and lower north-facing (BLN) sites were last burned by ground fires some 150–165 years ago (evidence from aging scarred and singed trees) and many of the canopy *Pseudotsuga* are over 500 years old at both sites, yet *Chrysolepis* has the highest density of seed-originated saplings and small trees in the understory and is represented at both sites by

the highest densities for trees of any transect. No correlation exists between total cover of all species and chinquapin cover, suggesting that successional stage of the forest has nothing to do with *Chrysolepis* density or cover.

On the three sites stems of giant chinquapins over 35 cm dbh appear to tolerate ground fires better than many similar-sized hardwoods (*Quercus* spp., *Acer macrophyllum*, *Lithocarpus*). At the Rough-Chinquapin site, where the largest chinquapin trees were noted, the last major fire occurred ca. 75–80 years ago and virtually all *Chrysolepis* over 45 cm dbh had at least small fire scars which were all or partially healed. The largest specimens (between 91 and 122 cm dbh) had cat-face scars and large sections of rotten core, indicating repeated fire damage. Most of the fire-scarred trees in mesic areas had single trunks, even those that were repeatedly damaged.

The successional reputation of giant chinquapin appears to come primarily from its ability to stump sprout following logging or crown fires (McKee ms.). Under these conditions it may outstrip young conifer growth for several years.

Atzet and Wheeler (1982, 1984) consider *Lithocarpus* as the major climax species where both soil and atmospheric moisture is plentiful at mid-slopes and elevations in the Siskiyou Mountains. Average elevation for their tanoak series is 945 m. Above the tanoak and below the white fir series (defined by Atzet and Wheeler as the area where *Abies concolor* dominates the sapling and seedling layers) lies the zone where *Chrysolepis* predominates. This zone is limited, but under the appropriate mesic conditions such as at transects BMN, BLN, and north slopes between 750 and 950 m at Rough-Chinquapin it may be considered as the hypothetical climax species based on its ability to reproduce and come to dominate in undisturbed situations.

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ANNOUNCEMENTS

NEW PUBLICATIONS

- BARBOUR, M. G. and J. MAJOR (eds.), *Terrestrial vegetation of California*, revised ed., California Native Plant Society, 909 12th St., Suite 116, Sacramento, CA 95814, Jan 1988, 1036 pp., with map (A. W. Küchler, “Vegetation map of California”) in pocket, illus., ISBN 0-943460-13-1 (hardbound), \$50.00. [With 26 chapters by 30 authors, a limited revision of the 1977 book.]
- BEEBLE, A. A., and collaborators, *Las Gramíneas de México*, vol. 2, Secretaría de Agricultura y Recursos Hidráulicos [México, D.F.], 1987, 344 pp., illus. (some color), no ISBN, paperbound, gratis (from COATECOCA, S.A.R.H. Manzanillo #83, Desp. 802, C.P. 06760, México, D.F.). [Arrangement of genera and species alphabetical; with ca. 40 genera: *Bambusa* through *Distichlis* (vol. 1 on the “A” genera appeared in 1983).]

THE HIGH ELEVATION FLORA OF MOUNT ST. HELENS, WASHINGTON

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ABSTRACT

The subalpine and alpine flora of Mount St. Helens is estimated to consist of about 95 species of vascular plants of which over 20 may have become locally extinct in 1980. In contrast, three nearby volcanoes contain two to three times as many species. The causes for this limited flora include intense and frequent volcanism that has locally extirpated some species and prevented others from reinvading. Mount St. Helens is very young and may not have existed when dispersal for alpine species was facilitated by full glacial conditions. It is isolated by 50 to 80 km of inhospitable lowlands from seed sources on other volcanoes. The area above treeline is small and lacks mesic and hydric habitats, thereby excluding many species capable of dispersing, but incapable of finding a suitable habitat. Mount St. Helens is biogeographically analogous to an oceanic island recently emerged from the sea, distant from potential seed source pools, and suffering the trauma of repeated catastrophes.

The eruptive history of Mount St. Helens is rich and well documented (Yamaguchi 1986) with at least eight major events occurring during the last 400 years. Prior to the eruption of 18 May 1980, this young volcano was the smallest and lowest (2950 m) of the volcanoes of the Pacific Northwest. The treeline of Mount St. Helens was abnormally low, ranging from about 1150 to 1350 m, depending on aspect (Lawrence 1938). Its elevation was reduced to 2550 m in 1980 by a huge debris avalanche and explosive lateral blast (see Rosenfeld 1980 for a description of events). In contrast, timberlines on neighboring volcanoes are at about 1800 m. Mount St. Helens is located at 46°12'N, 122°11'W and is 70 km north of Mount Hood (3428 m), 80 km west of Mount Adams (3752 m) and 52 km south-southwest of Mount Rainier (4393 m).

Prior to 1980, studies of subalpine vegetation on Mount St. Helens included only qualitative descriptions of xeric parkland and meadow communities developed on lava flows, pyroclastic flows, and mudflows (lahars) less than 500 years old (Crandell et al. 1975, Hoblitt et al. 1980). Unfortunately, there are no detailed floristic or vegetational studies that describe vegetation above treeline prior to the 1980 eruption.

This study evaluates what was known of the flora of Mount St.

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Helens prior to 1980, compares it to relevant floras of surrounding volcanoes, discusses reasons for its depauperate nature, and suggests that the most recent eruption has produced numerous local extinctions.

METHODS

The subalpine and alpine flora and meadow vegetation on the slopes of Mount St. Helens were poorly known prior to 1980. We used Hitchcock and Cronquist (1973) and Kruckeberg (1987) to develop an estimate of the flora prior to the massive eruptions that devastated the north flank of the volcano. The general characteristics of pre-eruption high elevation communities on Mount St. Helens can be inferred from the qualitative descriptions and checklists found in Piper (1906), St. John (1976, describing a collecting trip in 1925), and Kruckeberg (1987, describing a 3-day trip in 1979). In order to compare this subalpine flora with those of surrounding volcanoes, the following sources were consulted: for Mount Rainier, Dunwiddie (1983); for Mount Adams, Riley (1986); and for Mount Hood, Burnett (1986). Only species from these checklists likely to occur in subalpine or alpine habitats are included. Although Riley (1986) and Burnett (1986) excluded graminoids, we have included these families based on habitat descriptions in Hitchcock and Cronquist (1973) and personal observations.

Between 1980 and 1987 the first author investigated the flora above 1200 m for an average of 19 days per year. The second author averaged 21 days on the mountain each year between 1983 and 1987. Voucher specimens were prepared for all species encountered and are deposited in WTU.

Species were tabulated in several ways. All species encountered by any primary source on Mount St. Helens are listed by family. Species immigration and potential local extinction are thus indicated. Dispersal mechanisms are inferred from morphology (see Wood and del Moral 1987). Likely reasons for exclusion from the flora are estimated from knowledge of dispersal and habitat requirements.

In order to estimate the degree of disharmony in the Mount St. Helens flora, species were aggregated by plant family for each of the four volcanoes compared. Disharmony refers to an unbalanced distribution of species per family, relative to the flora of the region. A harmonious flora on Mount St. Helens would have about the same proportion of its species distributed among the families as on the other volcanoes.

RESULTS

The flora. The high elevation flora of Mount St. Helens is extremely poor, consisting of no endemics (St. John 1976, Kruckeberg 1987) and dominated by common species found at most high ele-

variations in the Pacific Northwest. Table 1 lists species reported for the higher elevation vegetation (Piper 1906, St. John 1976, del Moral 1983, del Moral and Wood pers. obs. 1980–87, Kruckeberg 1987). Species noted by Kruckeberg and not by St. John may be species that have invaded since 1925. The flora is very poorly-represented in those families dominated by mesophytes and well-represented in taxa with good dispersal mechanisms. Nomenclature follows that of Hitchcock and Cronquist (1973).

The 23 species noted by St. John or Kruckeberg, but not by del Moral, may be species that have been eliminated as a consequence of the 1980 eruption. (Negative evidence, in this case the non-observation of species, is always problematic.) These are indicated by an asterisk in Table 1 and include *Botrychium lanceolatum*, *Lewisia columbiana*, *Caltha biflora*, *Trautvetteria caroliniensis*, *Heuchera micrantha*, *Saxifraga arguta*, *Phyllodoce glanduliflora*, *Dodecatheon jeffreyi*, *Collomia debilis*, *Penstemon davidsonii*, *Valeriana sitchensis*, *Aster alpigenus*, *Erigeron peregrinus*, and *Luzula divaricata*.

The pre-eruptive subalpine and alpine flora on Mount St. Helens was dominated by species common to other Northwest volcanoes. Dominants included *Lupinus lepidus*, *L. latifolius*, *Eriogonum pyrolifolium*, *Polygonum newberryi*, *Luetkea pectinata*, *Saxifraga tolmiei*, *Phyllodoce empetriflora*, *Arctostaphylos uva-ursi*, *Juncus parryi*, *Spraguea umbellata*, and *Castilleja miniata*. Today, on the southern slopes of Mount St. Helens, these species are common meadow plants.

Impoverishment and disharmony. We are unaware of any biogeographic studies of non-equilibrium conditions on terrestrial islands. Table 2 summarizes the depauperate and disharmonious nature of the Mount St. Helens flora compared to the floras of Mount Rainier, Mount Adams, and Mount Hood. Subalpine and alpine species richness is estimated to be as follows: for Mount St. Helens, 95 species (including 23 species, 24%, now possibly extinct on the cone); for Mount Hood, 185 (Burnett 1986); for Mount Adams, 198 (Riley 1986); and for Mount Rainier, 261 (Dunwiddie 1983).

Prior to 1980, Mount St. Helens' flora was only about $\frac{1}{3}$ of that of Mount Rainier. Families with fewer than $\frac{1}{3}$ as many species are under-represented, whereas those with more than $\frac{1}{3}$ as many are over-represented. Based on this criterion, the following families are under-represented: Polypodiaceae, Salicaceae, Caryophyllaceae, Ranunculaceae, Brassicaceae, Saxifragaceae, Fabaceae, Onagraceae, Apiaceae, Boraginaceae, Scrophulariaceae, and Liliaceae. The Lycopodiaceae, Polygonaceae, Juncaceae, Cyperaceae, and Poaceae are over-represented.

DISCUSSION AND CONCLUSIONS

We postulate four reasons for low species richness and disharmony: 1) frequent disturbance causing relatively high local extinc-

TABLE 1. PLANT SPECIES COLLECTED OR OBSERVED ABOVE TIMBERLINE ON THE FLANKS OF MOUNT ST. HELENS. (Nomenclature has been modified to conform to Hitchcock and Cronquist, 1973. Piper's observations are from a table of "arctic-alpine species" plus higher elevation species from a table of "Hudsonian" species.) X = Species observed. * = Species not observed by authors or other field workers since 1980. ¹"Characteristic species"; Piper's list was not exhaustive. ²Species listed by these authors that are clearly not from subalpine habitats and tree species are omitted.

Plant family Species	Piper ¹ , ca. 1900	St. John ² , 1925	Krücke- berg ² , 1979	del Moral, 1980-1986
PTERIDOPHYTES				
Lycopodiaceae				
<i>Lycopodium sitchense</i>	X	X	X	X
<i>L. annotinum</i>	—	X	—	*
Ophioglossaceae				
<i>Botrychium lanceolatum</i>	—	X	X	*
Polypodiaceae				
<i>Cryptogramma crispa</i>	—	X	X	X
Selaginellaceae				
<i>Selaginella wallacei</i>	—	X	—	*
GYMNOSPERMS				
Cupressaceae				
<i>Juniperus communis</i>	X	X	X	X
ANGIOSPERMS—DICOTS				
Apiaceae				
<i>Lomatium martindalei</i>	X	X	X	X
Asteraceae				
<i>Achillea millefolium</i>	—	X	X	X
<i>Agoseris aurantiaca</i>	X	X	—	X
<i>A. glauca</i>	—	—	—	X
<i>Anaphalis margaritacea</i>	—	X	X	X
<i>Antennaria microphylla</i>	X	X	X	X
<i>A. lanata</i>	—	—	X	X
<i>Arnica latifolia</i>	X	X	X	X
<i>A. cordifolia</i>	—	—	—	X
<i>Aster alpigenus</i>	X	X	—	*
<i>A. ledophyllus</i>	X	X	X	X
<i>Erigeron peregrinus</i>	—	X	—	*
<i>Eriophyllum lanatum</i>	—	X	—	X
<i>Hieracium albiflorum</i>	—	X	X	X
<i>H. gracile</i>	—	—	X	X
<i>Luina hypoleuca</i>	—	X	X	X
<i>Microseris alpestris</i>	X	X	X	X
Campanulaceae				
<i>Campanula rotundifolia</i>	—	X	—	X
Caryophyllaceae				
<i>Silene parryi</i>	—	X	—	X

TABLE 1. CONTINUED.

Plant family Species	Piper ¹ , ca. 1900	St. John ² , 1925	Krucke- berg ² , 1979	del Moral, 1980-1986
Crassulaceae				
<i>Sedum oreganum</i>	—	X	—	*
Ericaceae				
<i>Arctostaphylos uva-ursi</i>	—	X	X	X
<i>Phyllodoce empetriformis</i>	X	X	X	X
<i>Phyllodoce glanduliflora</i>	X	X	X	*
<i>Vaccinium scoparium</i>	X	X	—	X
<i>Vaccinium membranaceum</i>	—	—	—	X
Fabaceae				
<i>Lupinus latifolius</i>	—	X	X	X
<i>L. lepidus</i> var. <i>lobbii</i>	X	X	X	X
Gentianaceae				
<i>Gentiana calycosa</i>	—	—	—	X
Hydrophyllaceae				
<i>Phacelia hastata</i>	—	X	X	*
Onagraceae				
<i>Epilobium angustifolium</i>	—	X	X	X
<i>E. alpinum</i>	—	X	—	X
Polemoniaceae				
<i>Collomia debilis</i>	—	X	—	*
<i>Linanthastrum nuttallii</i>	—	—	—	X
<i>Phlox diffusa</i>	X	X	X	X
Polygonaceae				
<i>Eriogonum pyrolifolium</i>	X	X	X	X
<i>E. ovalifolium nivale</i>	—	—	—	X
<i>Polygonum newberryi</i>	X	X	X	X
<i>P. minimum</i>	—	X	—	X
Portulacaceae				
<i>Lewisia columbiana</i>	X	X	—	*
<i>Spraguea umbellata</i>	X	X	X	X
Primulaceae				
<i>Dodecatheon jeffreyi</i>	—	X	—	*
Ranunculaceae				
<i>Aquilegia formosa</i>	—	X	—	X
<i>Caltha biflora</i>	X	X	—	*
<i>Trautvetteria caroliniensis</i>	—	—	X	*
Rosaceae				
<i>Fragaria virginiana</i>	—	X	X	X
<i>Luetkea pectinata</i>	—	X	X	X
<i>Potentilla arguta</i>	—	—	—	X
<i>Rubus lasiococcus</i>	X	X	X	X
<i>Sibbaldia procumbens</i>	—	X	X	X
<i>Sorbus sitchensis</i>	X	X	X	X
<i>Spiraea densiflora</i>	X	X	X	X

TABLE 1. CONTINUED.

Plant family Species	Piper ¹ , ca. 1900	St. John ² , 1925	Krucke- berg ² , 1979	del Moral, 1980-1986
Salicaceae				
<i>Salix barclayi</i>	—	X	X	X
Saxifragaceae				
<i>Heuchera micrantha</i>	X	X	X	*
<i>Saxifraga arguta</i>	—	X	—	*
<i>S. tolmiei</i>	X	X	X	X
Scrophulariaceae				
<i>Castilleja miniata</i>	—	X	X	X
<i>Penstemon cardwellii</i>	—	—	X	X
<i>P. confertus</i>	—	X	—	X
<i>P. davidsonii</i> var. <i>menziesii</i>	X	—	—	*
<i>P. serrulatus</i>	—	X	—	*
Valerianaceae				
<i>Valeriana sitchensis</i>	X	X	X	*
Violaceae				
<i>Viola adunca</i>	—	—	—	X
ANGIOSPERMS—MONOCOTS				
Cyperaceae				
<i>Carex mertensii</i>	—	X	—	X
<i>C. pachystachya</i>	—	—	—	X
<i>C. phaeocephala</i>	—	X	—	X
<i>C. rossii</i>	—	X	X	X
<i>C. spectabilis</i>	X	X	X	X
Juncaceae				
<i>Juncus parryi</i>	—	X	X	X
<i>J. drummondii</i>	—	—	—	X
<i>Luzula divaricata</i>	X	X	—	*
<i>L. piperi</i>	—	—	X	X
Liliaceae				
<i>Smilacina racemosa</i>	—	X	X	X
<i>S. stellata</i>	—	X	X	X
<i>Xerophyllum tenax</i>	—	X	—	X
Poaceae				
<i>Agrostis diegoensis</i>	—	—	X	X
<i>A. exarata</i>	—	X	—	X
<i>A. variabilis</i>	—	X	—	*
<i>Bromus carinatus</i>	—	—	—	X
<i>Calamagrostis sesquiflora</i>	—	X	—	*
<i>Danthonia intermedia</i>	—	X	X	X
<i>D. spicata</i>	—	X	—	*
<i>Festuca occidentalis</i>	X	X	—	X
<i>Festuca viridula</i>	—	—	X	*
<i>Phleum alpinum</i>	—	X	X	X
<i>Poa incurva</i>	—	X	—	X
<i>Sitanion hystrix</i>	—	X	X	X
<i>S. jubatum</i>	—	—	X	X
<i>Stipa occidentalis</i>	—	X	—	X
<i>Trisetum spicatum</i>	X	X	—	X

TABLE 2. NUMBER OF SPECIES IN PLANT FAMILIES ON FOUR VOLCANOES: MOUNT ST. HELENS, MOUNT RAINIER (Dunwiddie 1983), MOUNT ADAMS (Riley 1986), AND MOUNT HOOD (Burnett 1986). Parenthetical values are post-1980 estimates, where different. ¹Lycopodiaceae and Selaginellaceae. ²Ophioglossaceae and Polypodiaceae.

Family	Mount St. Helens	Mount Rainier	Mount Adams	Mount Hood
Fern allies ¹	3 (2)	4	3	3
Ferns ²	2 (1)	6	5	3
Cupressaceae	1	1	1	1
ANGIOSPERMS—DICOTS				
Apiaceae	1	5	5	6
Asteraceae	16 (14)	50	35	27
Boraginaceae	0	2	0	2
Brassicaceae	0	14	8	5
Campanulaceae	1	1	1	1
Caryophyllaceae	1	9	5	4
Crassulaceae	1 (0)	3	2	1
Droseraceae	0	1	1	1
Ericaceae	5 (4)	11	9	7
Fabaceae	2	7	4	5
Gentianaceae	1	1	1	1
Hippuridaceae	0	1	0	0
Hydrophyllaceae	1 (0)	3	2	2
Hypericaceae	0	1	1	1
Onagraceae	2	11	6	8
Polemoniaceae	3 (2)	9	7	7
Polygonaceae	4	9	7	8
Portulacaceae	2 (1)	5	3	2
Primulaceae	1 (0)	3	2	2
Ranunculaceae	3 (2)	13	8	9
Rosaceae	7	15	12	10
Salicaceae	1	4	2	3
Saxifragaceae	3 (1)	15	9	8
Scrophulariaceae	5 (3)	20	18	17
Valerianaceae	1 (0)	1	1	1
Violaceae	1	1	1	1
ANGIOSPERMS—MONOCOTS				
Cyperaceae	5	13	10	9
Juncaceae	4 (3)	6	4	3
Liliaceae	3	9	5	7
Poaceae	15 (11)	20	19	19
Orchidaceae	0	2	1	1
Totals	95 (72)	276	198	185

tion rates; 2) low immigration rates due to isolation and ineffective dispersal mechanisms (e.g., mammals, ants, water, and gravity); 3) the immaturity of the volcano resulting in poor soils; and 4) a lack of mesic and hydric habitats.

The flora may have increased during the interval between major eruptions (1852 to 1980). For example, Piper (1906) listed only 45 species for the upper slopes of Mount St. Helens. Lawrence (1938,

1939) found 80 vascular plant species on pumice between 1200 and 2200 m. Lawrence stated that at least some were recent immigrants and that new species should be expected to invade each year. Kruckeberg (1987) stated that 70 vascular plants species common in other subalpine and alpine regions of the Cascades do not occur on Mount St. Helens. In contrast, species in groups with effective long-distance dispersal mechanisms, such as lycopods, composites, grasses, sedges and rushes, are well represented. The vegetation of subalpine meadows on Mount St. Helens is characterized by widely distributed species common to Northwestern volcanoes, whereas many other common species are lacking.

Species strangely absent from Mount St. Helens are noted in Table 3, along with potential reasons for their absence, related to those factors stated above. In addition, several species may have succumbed to the most recent disturbance. The list is meant to illustrate reasons potentially excluding a species from a habitat and should not be construed as definitive. Species from the list of Kruckeberg (1987) (except for three known to exist in 1979) have been categorized as follows: 18 of 67 species appear to be absent primarily because their dispersal mechanisms are effective for only short distances. The bulk of the species (27 of 67) appear limited both by inefficient dispersal and the absence or small size of suitable habitats. The true alpine zone is small on this volcano, especially since 1980. Lush meadow habitats, such as the extensive meadows near Paradise on Mount Rainier, have never been common and today are virtually absent. Glaciers that existed on steep slopes were nearly completely removed. Their remnants apparently did not support any distinct wetland vegetation. Bogs do not exist on or near the cone. Therefore lush meadow species (*Anemone occidentalis*) and bog dwellers (*Kalmia microphylla*) do not occur. A few species, such as *Alliumcernuum*, may tolerate drought, but require better developed soils than occur. Twenty species have effective dispersal mechanisms, but are absent primarily for reasons related to their special habitat requirements. The lack of a sizable, stable alpine habitat may exclude genera like *Empetrum* and *Dryas*. Wet meadow species are absent because of insufficient moisture. The absence of stable, dry soil and very acid soils may limit other species. Species such as *Vaccinium deliciosum* are expected; their absence may be due only to chance. Species other than those mentioned by Kruckeberg (1987) might be expected, but are lacking for one or more of the reasons discussed below.

Although none of the studies cited above is complete, each implies a depauperate flora. Incomplete collecting may account for some gaps in earlier studies since these concentrated on the north slopes. However, species confined to the north slope may indeed now be absent from the volcano.

It is likely that low richness and disharmony of the flora above

TABLE 3. SUMMARY OF PROBABLE CAUSES FOR THE ABSENCE OF COMMON SPECIES FROM MOUNT ST. HELENS VOLCANO.

Reason	Total	Examples
Primarily dispersal	18	
No special mechanism	12	<i>Arabis</i> spp., <i>Draba aureola</i> , <i>Arenaria</i> spp., <i>Saxifraga</i> spp., <i>Smelowskia</i> spp., <i>Thlaspi fendleri</i> , <i>Phacelia sericea</i> , <i>Polemonium elegans</i>
Mammals	6	<i>Agropyron</i> spp., <i>Deschampsia atropurpurea</i> , <i>Eriogon</i> spp.
Dispersal and habitat	27	
Lack of alpine habitat	1	<i>Oxyria digyna</i>
Too dry	24	<i>Anemone</i> spp., <i>Kalmia microphylla</i> , <i>Erythronium montanum</i> , <i>Ranunculus</i> spp., <i>Dodecatheon jeffreyi</i> , <i>Douglasia laevigata</i> , <i>Solidago multiradiata</i> , <i>Veronica cusickii</i> , <i>Silene</i> spp., <i>Thalictrum</i> spp.
Lack of suitable soil	2	<i>Allium cernuum</i> , <i>Spiraea betulifolia</i>
Primarily habitat	20	
Lack of alpine habitat	6	<i>Artemisia norvegica</i> , <i>Silene acaulis</i> , <i>Salix</i> spp., <i>Dryas octopetala</i> , <i>Empetrum nigrum</i>
Too dry	10	<i>Epilobium latifolium</i> , <i>Polypodium hesperium</i> , <i>Habenaria dilatata</i> , <i>Aster alpigenus</i> , <i>Pedicularis</i> spp., <i>Senecio triangularis</i> , <i>Saussurea americana</i>
Lack of suitable soil	4	<i>Sedum</i> spp., <i>Cheilanthes gracillima</i> , <i>Cassiope mertensiana</i>
Chance	2	<i>Vaccinium deliciosum</i> , <i>Haplopappus lyallii</i>

timberline on Mount St. Helens result from a combination of several factors. Frequent eruptive disturbances probably caused the local extinction of many species. *Caltha biflora*, *Dodecatheon jeffreyi*, and *Festuca viridula* are among species probably extirpated from the cone in 1980. These are species not known from the south half of the cone, and they generally occur in mesic habitats.

The youth and small size of the volcano have several important consequences. Some species may have reached other alpine areas during glacial maxima at a time when Mount St. Helens either did not exist or lacked high elevation habitats. Poorly developed substrates preclude the development of habitats for mesophytic species. Over time, soil development will occur so that species common, for example, at Sunrise on Mount Rainier, may be able to grow. Such species include *Potentilla flabellifolia* and *Veronica cusickii*. Many families under-represented on Mount St. Helens are primarily mesophytes.

Restricted habitats subject the flora to several processes likely to reduce richness. 1) Disturbances may totally eliminate certain habitats; 2) existing habitats are smaller and less diverse and therefore less likely to have as many species due to simple species-area effects;

3) populations of rare species will be small and of limited distribution and therefore more susceptible to elimination; and 4) small habitats are less likely to intercept invading seeds than large habitats. In addition, species unable to withstand burial by tephra and other mild impacts may succumb whereas more tolerant species survive. Long distances from seed sources also contribute to limited recolonization from surrounding areas, despite the 123-year dormant period preceding the 1980 eruption. Nearby subalpine and alpine communities on the Old Cascades nonvolcanic landscape, notably on Mount Margaret and Strawberry Mountain, probably were depauperate because they were decimated by thick tephra deposited in A.D. 1480 (Yamaguchi 1986). As a result, many seed sources of the pre-1980 landscape may have been as distant as the nearest volcanoes.

The frequency of major disturbances on Mount St. Helens is such that the flora appears to be far below its equilibrium richness (see Malanson 1984). Studies of isolated young woodlands (less than 350 years old) in Britain (Peterken and Game 1984) suggest first that such woodlands are depauperate and disharmonious and second that they acquire most of their species within 20 years. Even minor isolation serves to restrict colonization rates dramatically.

The balance between frequent episodic local extinction and presumably gradual colonization on Mount St. Helens, combined with small area and an immature landscape, has produced a monotonous flora remarkably limited in richness. The 1980 eruptions may have contributed to this impoverishment, with as many as 23 of 95 species being eliminated in 1980.

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ANNOUNCEMENTS

NEW PUBLICATIONS

- DAVIS, S. D., S. J. M. DROOP, P. GREGERSON, L. HENSON, C. J. LEON, J. L. VILLA-LOBOS, H. SYNGE, and J. ZANTOVSKA, *Plants in danger: What do we know?*, International Union for Conservation of Nature and Natural Resources, Avenue du Mont-Blanc, CH-1196 Gland, Switzerland, 1986, xlv, 461 pp., unillust., ISBN 2-88032-707-5 (paperbound), SFr 40.50. [On Canada, Mexico, the United States, and everywhere else. Arrangement by country, including for each data on geography, population number, floristics, and vegetation, plus references (often many), and, as relevant, information on threatened plants, laws protecting plants, and addresses for botanic gardens and other organizations. For review see C. J. Humphries, *Watsonia* 17:106.]
- GRIFFIN, J. R., P. M. McDONALD, and P. C. MUICK (compilers), *California oaks: A bibliography*, U.S.D.A. Pacific Southwest Forest and Range Experiment Station, General Technical Report PSW-96, pp. [i], 1–37, May 1987, unillust., no ISSN, gratis (from Pacific Southwest Forest and Range Experiment Station, P.O. Box 245, Berkeley, CA 94701). [Biblio. of 768 entries, with subject indices.]

CHROMOSOME NUMBERS IN THE ANNUAL *MUHLENBERGIA* (POACEAE)

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ABSTRACT

Chromosome numbers were obtained from field-collected microsporocytes and root-tip preparations from greenhouse-grown specimens for 25 species of annual *Muhlenbergia* sensu lato. Nine of these counts are first reports: *M. annua* ($2n=20$), *M. biloba* ($n=8$), *M. eludens* ($n=20$), *M. fragilis* ($n=10$), *M. pectinata* ($n=10$), *M. schmitzii* ($n=20$), *M. shepherdii* ($n=8$), *M. sinuosa* ($n=10, 12$), and *M. tenuissima* ($n=10$). Besides sharing a haploid number of $n=8$, *M. biloba* and *M. shepherdii* also have large chromosomes unlike those of the other species. Both appear to be misplaced in *Muhlenbergia*: *M. biloba* is better treated as *Bealia mexicana* and *M. shepherdii* probably should be transferred to *Blepharoneuron*.

RESUMEN

El número de cromosomas de 25 especies de *Muhlenbergia* sensu lato se obtuvieron de muestras obtenidas de esporófitos recogidos en el campo o de preparaciones de ápices de la raíces de ejemplares cultivados en invernaderos. Se reporta por primera vez el número de cromosomas de 9 especies diferentes. Estas son las siguientes: *M. annua* ($2n=20$), *M. biloba* ($n=8$), *M. eludens* ($2n=20$), *M. fragilis* ($n=10$), *M. pectinata* ($n=10$), *M. schmitzii* ($2n=20$), *M. shepherdii* ($n=8$), *M. sinuosa* ($n=10, 12$), y *M. tenuissima* ($n=10$). *Muhlenbergia biloba* y *M. shepherdii* se destacan de otras especies al tener un número haploide de 8 cromosomas y al tener cromosomas de tamaño mayor. Parece ser que ninguna de estas dos últimas especies pertenecen en el género *Muhlenbergia*: *M. biloba* se debe considerar como *Bealia mexicana* y *M. shepherdii* se debe transferir al género *Blepharoneuron*.

Muhlenbergia Schreb. (Chloridoideae: Eragrostideae) comprises over 160 species (Clayton and Renvoize 1986), most of which occur in arid lands of the New World. Of the 32 annual species, 31 taxa occur in Mexico, 14 of which also occur in the southwestern United States, and a single species is restricted to Guatemala. Although several alliances within the annuals are apparent, some groups appear to be paraphyletic and closely related to several perennial *Muhlenbergia*.

Chromosome counts reported here are part of a long-range systematic study on the annual species of *Muhlenbergia* (Peterson and Rieseberg 1987, Peterson et al. 1988, Peterson 1989). Chromosome counts for only 16 species had been reported (Myers 1947, Tateoka

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1962, Gould 1965, 1966, Reeder 1967, 1968, Gould and Soderstrom 1970, Pohl and Davidse 1971, Davidse and Pohl 1974, Hatch 1980). I determined additional chromosome counts to help provide baseline data for a systematic study of the group. Chromosome data may also be valuable for inferring phylogeny and interpreting patterns of evolution (Clausen et al. 1945).

MATERIALS AND METHODS

Floral buds were field collected and fixed in ethanol-acetic acid (3:1, V:V) prior to storage under refrigeration in 70% ethanol. Meiotic chromosome counts were obtained from aceto-carmine squashes of pollen mother cells. Root tips were collected from greenhouse-grown specimens and subsequently treated in 0.002 M 8-hydroxyquinoline (4 hr), ethanol-acetic acid fixative (2 hr), glusulase (45 min), and 0.2 N hydrochloric acid (2 min) before being squashed in aceto-carmine (Soltis 1980). Representative cells were recorded with sketches and photographed using a Nikon Biophot, phase-contrast microscope, using 35 mm Kodak technical pan 2415 film. Chromosome number determinations were based on observations of 15 or more cells from at least three individuals per population. Vouchers of the plants counted are deposited in WS.

RESULTS

A total of 67 chromosome counts were made, representing 25 species of annual *Muhlenbergia* sensu lato. Chromosome number, locations, and collection numbers are listed in Table 1 for each of the 25 species. Chromosome numbers for the following nine species are first reports: *M. annua* ($2n=20$), *M. biloba* ($n=8$), *M. eludens* ($n=20$), *M. fragilis* ($n=10$), *M. pectinata* ($n=10$), *M. schmitzii* ($n=20$), *M. shepherdii* ($n=8$), *M. sinuosa* ($n=10, 12$), and *M. tenuissima* ($n=10$). The chromosome numbers of *M. brevis* ($n=10$), *M. ciliata* ($n=10$), *M. minutissima* ($n=30$), *M. crispiseta* ($n=10$), *M. depauperata* ($n=10$), *M. diversiglumis* ($n=10$), *M. filiformis* ($n=9$), *M. implicata* ($n=10$), *M. microsperma* ($n=10$), *M. ramulosa* ($n=10$), *M. strictior* ($n=10$), *M. tenella* ($n=10$), *M. tenuifolia* ($n=20$), *M. texana* ($n=20$), and *M. vaginata* ($n=9$) are concordant with previous reported counts (Meyers 1947, Tateoka 1962, Gould 1965, 1966, Reeder 1967, 1968, Gould and Soderstrom 1970, Pohl and Davidse 1971, Davidse and Pohl 1974, Hatch 1980). *Muhlenbergia sinuosa* has two different chromosome races with two $n=12$ populations from Cochise and Santa Cruz counties, Arizona and two $n=10$ populations from Grant County, New Mexico and Chihuahua, Mexico. The meiotic chromosome count for *M. pusilla* ($n=15$) substantiated a previous somatic count of $2n=30$ for the same species (Reeder 1968). Some microsporocytes of three populations of *M. strictior*

TABLE 1. CHROMOSOME COUNTS IN THE ANNUAL *Muhlenbergia* SENSU LATO. Populations are arranged alphabetically by species and locality. All collections are those of the author and C. R. Annable. Vouchers are deposited in WS. Unless otherwise noted, all counts were obtained from microsporocytes.

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- M. annua* (Vasey) Swallen $2n=20$. Mexico, Chihuahua, nw. of Hernandez Javales, 4053; Durango, w. of Navios, 4582 (root tip count).
- M. biloba* A. S. Hitchc. $n=8$. Mexico, Durango, sw. of El Ojito, 4570.
- M. brevis* C. Goodding $n=10$. Mexico, Chihuahua, s. of Hernandez Javales, 4041; n. of Cuesta Blanca, 4047; sw. of Madera, 4051; ne. of El Vergel, 4061; Durango, w. of Río Chico Crossing, 4094.
- M. ciliata* (H.B.K.) Kunth $n=10$. Mexico, Chihuahua, ne. of El Vergel, 4080 (some cells at $n=9$); Durango, w. of Río Chico Crossing, 4093; e. of El Salto, 4119; Michoacán, s. of Uruapan, 4619; Sinaloa, nw. of Surutato, 4165.
- M. crispiseta* A. S. Hitchc. $n=10$. Mexico, Durango, sw. of El Ojito, 4571.
- M. depauperata* Scribn. $n=10$. Mexico, Chihuahua, n. of Villa Matamoros, 4082; s. of Villa Matamoros, 4083; Zacatecas, nw. of Fresnillo, 4596.
- M. diversiglumis* Trin. $n=10$. Mexico, Sinaloa, e. of Santa Lucia, 4147.
- M. eludens* C. Reeder $n=20$. Mexico, Durango, w. of Río Chico Crossing, 4096. USA, AZ, Santa Cruz Co., sw. of Canelo, 4018.
- M. filiformis* (Thurb.) Rydb. $n=9$. USA, AZ, Apache Co., e. of McNary, 3994; Washington, Klickitat Co., Wash. St. Salmon Hatchery, 3987.
- M. fragilis* Swallen $n=10$. Mexico, Chihuahua, w. of Parral, 4554. USA, AZ, Santa Cruz Co., Sycamore Canyon, 4024.
- M. implicata* (H.B.K.) Kunth $n=10$. Mexico, Chihuahua, ne. of El Vergel, 4079; Durango, s. of El Ojito, 4566; Oaxaca, se. of Sinaxtla, 4670.
- M. microsperma* (DC.) Kunth. $n=10$. USA, AZ, Santa Cruz Co., Sycamore Canyon, 4023; NV, Clark Co., Lake Mead, 3067.
- M. minutissima* (Steud.) Swallen [incl. *M. confusa* (Fourn.) Swallen] $n=30$. Mexico, Chihuahua, sw. of Colonia Juarez, 4037; Durango, w. of Río Chico Crossing, 4097; Mexico, w. of Toluca, 4634. USA, AZ, Apache Co., n. of Sunrise Lake, 3998.
- M. pectinata* C. Goodding $n=10$. Mexico, Durango, s. of Durango, 4089; w. of El Salto, 4132; w. of La Ciudad, 4135, 4139, 4141; Sinaloa, s. of Surutato, 4151, 4152.
- M. pusilla* Steud. [incl. *M. pulcherrima* Scribn.] $n=15$. Mexico, Chiapas, nw. of Motozintla de Mendoza, 4712; Chihuahua, sw. of El Vergel, 4073.
- M. ramulosa* (H.B.K.) Swallen [incl. *M. wolfii* (Vasey) Rydb.] $n=10$. Mexico, Chihuahua, ne. of El Vergel, 4064. USA, AZ, Cochise Co., Rustler Campground, 4011.
- M. schmitzii* Hack. $n=20$. Mexico, Michoacán, w. of Ciudad Hidalgo, 4631.
- M. shepherdii* (Vasey) Swallen $n=8$. Mexico, Durango, w. of El Salto, 4122, s. of El Ojito, 4561.
- M. sinuosa* Swallen $n=10, 12$. Mexico, Chihuahua, w. of Tomochic, 4540 ($n=10$). USA, AZ, Cochise Co., Rucker Lake, 4013 ($n=12$); Santa Cruz Co., sw. of Canelo, 4020 ($n=12$); NM, Grant Co., San Lorenzo, 4008 ($n=10$).
- M. strictior* Scribn. $n=10$. Mexico, Chihuahua, s. of Hernandez Javales, 4039 (some cells at $n=9$), 4043; w. of Tomochic, 4553; w. of La Junta, 4054 (some cells at $n=9$); Durango, s. of El Ojito, 4563 (some cells at $n=9$); w. of Navios, 4584.
- M. tenella* (H.B.K.) Trin. $n=10$. Mexico, Chiapas, s. of Frontera Comalapa, 4704.
- M. tenuifolia* (H.B.K.) Trin. $n=20$. Mexico, Chihuahua, ne. of Parral, 4059; s. of Villa Matamoros, 4085.
- M. tenuissima* (Presl) Kunth $n=10$. Mexico, Jalisco, s. of Yahualica, 4062.
- M. texana* Buckl. $n=20$. Mexico, Durango, w. of Navios, 4108. USA, AZ, Santa Cruz Co., sw. of Canelo, 4019; Sycamore Canyon, 4028.
- M. vaginata* Swallen $n=9$. Mexico, Durango, w. of El Salto, 4124, 4591; w. of Navios, 4587.
-

and one population of *M. ciliata* exhibited irregularity ($n=9$) suggesting facultative aneuploidy. However, most microsporocytes of these populations had normal bivalents during meiosis ($n=10$). The chromosomes of *M. biloba* and *M. shepherdii* were significantly larger than those of any other species in this survey.

DISCUSSION

Twenty of the species investigated have a basic number of $x=10$ which is in agreement with the previously reported base number for the genus (Darlington and Wylie 1956, Pohl and Mitchell 1965). *Muhlenbergia filiformis* and *M. vaginata* have a base number of $x=9$ which suggests a close relationship with *Sporobolus*, also $x=9$. This base number is perhaps a result of stabilized aneuploidy or dysploidy. The haploid number of $n=15$ for *M. pusilla* is unusual in the genus. Individuals of *M. pusilla* show tremendous morphological variation within and among natural populations. Lemmas and awns vary from 2.0–4.2 mm and 0–22 m long, respectively. The chromosome number and varying morphological forms suggest that these plants may be triploid and completely apomictic (Reeder 1968).

The two counts of $n=8$ for *M. biloba* and *M. shepherdii*, coupled with their large chromosome size compare with other *Muhlenbergia*, suggest that these taxa are misplaced in this genus. *Muhlenbergia biloba*, originally described as *Bealia mexicana* by Scribner in Hackel (1890), is perhaps best retained in its own monotypic genus. Cytologically, *M. biloba* shows close affinities with *Dasyochloa* Rydb. and *Erioneuron* Nash, both $x=8$. Lemma morphology among these taxa is very similar. All possess three-nerved, emarginate to bilobed, and often awned lemmas with pilose hairs associated with either the nerves, margins, and/or lower $\frac{2}{3}$ of the lemma. However, *M. biloba* [*Bealia mexicana*] differs from *Dasyochloa* and *Erioneuron* by being single-flowered and annual in nature.

Muhlenbergia shepherdii seems more closely related to the monotypic genus *Blepharoneuron* Nash than to other members of *Muhlenbergia*. These two taxa share the following features: chromosome number of $n=8$, strongly ribbed leaf blades, indistinguishable leaf anatomy, 1-flowered spikelets, subequal glumes almost as long as the floret, rounded lemmas with pilose margins and midnerve, and paleas that are densely (appressed in *M. shepherdii*) villous on and between the keel. I plan to transfer this species into *Blepharoneuron*.

The evidence from cytology, coupled with anatomy and morphology suggests that the annual species of *Muhlenbergia* sensu lato form at least three phylogenetically distinct lines. *Muhlenbergia biloba* [*Bealia mexicana*] and *M. [Blepharoneuron] shepherdii* each seem to form two distant but related lines, whereas all other members with $x=9$, 10 form a possible third lineage.

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ASTRAGALUS NUTRIOSENSIS (FABACEAE):
A NEW SPECIES FROM EASTERN ARIZONA

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ABSTRACT

A new species of *Astragalus* from the White Mountains of Arizona is described and its possible relationships discussed. Its unusual morphology combines features found in two western North American sections of the genus. Morphological evidence suggests it is most closely related to species in section *Mollissimi*, although it possesses several character states that are unusual in the context of that section.

A distinctive new species of *Astragalus* has recently been discovered among the mesas along Nutrioso Creek in the White Mountains of eastern Arizona. Easily overlooked because of its dwarf habit and cryptic flowers, it remains a difficult species to study in the field. Two relatively large populations several kilometers apart were found following the wet spring of 1987. The spring of 1988 was unusually dry; population sizes were lower, and the plants were evidently suffering from severe water stress, producing fewer leaves and flowers than in the previous year. Preliminary indications are that the species is a narrow endemic, but a complete survey of its distribution must await a future, more favorable season.

Astragalus nutriosensis Sanderson, sp. nov. (Fig. 1)

Habitu *A. mollissimus* var. *matthewsii* (Wats.) Barneby, sed pedunculis brevissimus; floribus perangustis longis, niveis, apicibus subroseis; fructibus parvis (8–10 mm longis), bilocularibus perfecte, in duo dimidia inaperta findentibus.

Dwarf, tufted, acaulescent, perennial herbs from a well-developed, short but broad, knotty caudex on a simple taproot. Upper surface of leaflets glabrescent-green; herbage otherwise cinereous and covered with spreading, basifixed hairs up to 2 mm long. Leaves 3–11 cm long; petiole usually at least half that length; leaflets 4–8 mm long, 1.5–4 mm wide, in 5–9 pairs, obovate or elliptic, acute or obtuse at apex; stipules 3–9 mm long, deltoid or lanceolate, with prominent green midrib and scarious or hyaline margins. Peduncles (rachises) 0–2(–5) cm long, almost always much shorter than the leaves, and often appearing obsolete, not elongating in fruit; racemes very short, up to 0.6 cm, (1–)2–5(–7)-flowered, the flowers strongly ascending; bracts 2–5 mm long, greenish, narrowly lanceolate; ped-

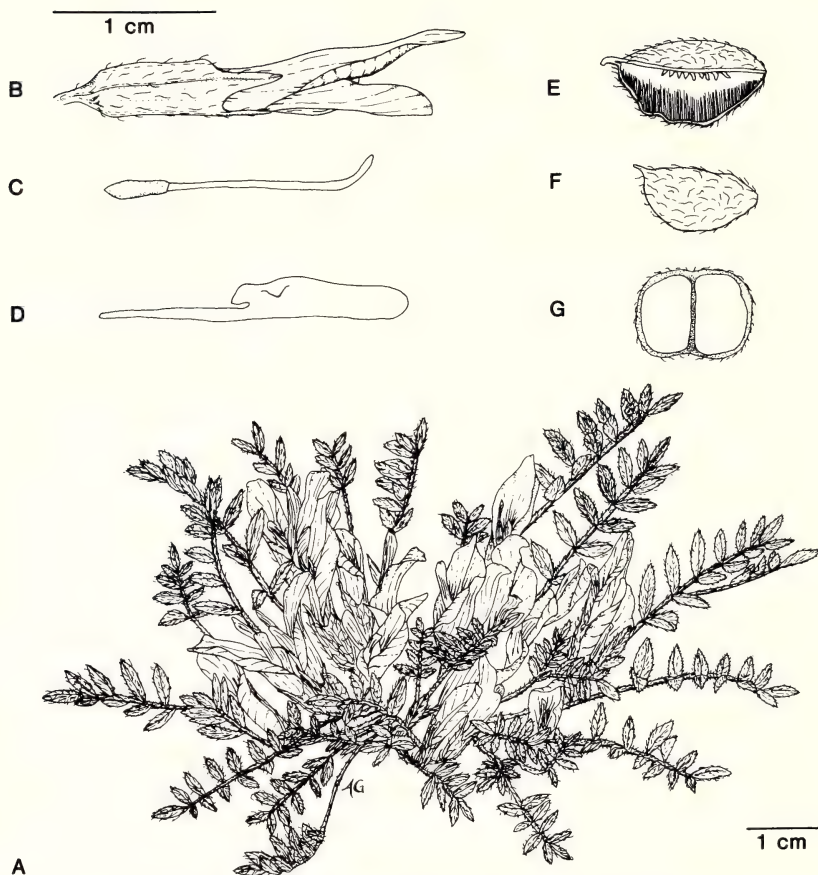


FIG. 1. *Astragalus nutriosensis* Sanderson (Sanderson 551). A. Habit. B. Flower. C. Gynoeceium. D. Wing petal. E. Longitudinal view of "dehiscent" pod showing complete septum with funicular scars. F. Pod, external view. G. Pod, transverse section.

icels 2–4 mm long. Calyx 11–14 mm long, 2–3 mm wide at base of teeth, narrowly cylindric, pilose with spreading hairs, subsymmetrically attached at base, the receptacle not oblique. Petals white with pink-purple veins and/or tips; banner 20–23 mm long, about 6 mm wide, oblanceolate and emarginate at apex, little recurved (less than 30 degrees); wings 19–22 mm long, blade about 10 mm long, of uniform, narrow width (2 mm), rounded at apex and not at all incurved; keel significantly shorter than the wings, about 14–17 mm long, blade of keel 5–6 mm long, obtuse and longer than wide. Anthers about 0.5 mm long, filaments incurved only very distally.

Ovary unusually short at anthesis (about one-fifth the entire length of the gynoecium), the septal intrusion only partially developed at this time; ovules about 20. Pods small, 8–10 mm long, 6–8 mm wide, almost beakless, broadly half-elliptic in profile, subterete in cross-section, the ventral suture slightly depressed proximally, sessile on receptacle (estipitate), on the very short peduncles, close to the caudex, readily deciduous; valves papery, thin, brownish-gray and covered with spreading hairs, septum complete throughout; dehiscence of fruit by fracture of pod into two closed, carpel-like halves, each half retaining one side of the folded endocarp, the seeds probably eventually escaping through weathered septum walls.

TYPE: USA, Arizona, Apache Co., on hillside ne. of intersection of AZ hwy. 666 and Apache Co. hwy. 116, about 9.5 km n. of Nutrioso, 2270 m (7460 ft), 25 May 1987, *Sanderson 551* (Holotype: ARIZ; isotypes: NY, others to be distributed).

PARATYPE: USA, Arizona, Apache Co., nw. of intersection of AZ hwy. 666 and Apache Co. hwy. 130, 2310 m (7600 ft), 6 km se. of Springerville, and about 8 km from the type locality, 28 May 1988, *Sanderson 706* (ARIZ).

Ecology and distribution. Known only from two localities along Nutrioso Creek in the White Mountains of eastern Arizona. Rare at the type locality, but fairly common at the second locality. Found on volcanic silty-clay soils on gently sloping hillsides; associated with *Bouteloua gracilis* (H.B.K.) Lag. and *Gutierrezia sarothrae* (Pursh) Britt. & Rusby in open grassland, sometimes among pinyon and juniper on slopes. Sympatric with *Oxytropis lambertii* Greene, *Astragalus humistratus* A. Gray, *A. brandegei* Porter, and *A. mollissimus* var. *matthewsii* (S. Wats.) Barneby. Flowering in May, fruiting by late May or June.

Phylogenetic relationships. Several morphological characters of *A. nutriosensis* are shared by certain members of sections *Argophylli* A. Gray and *Mollissimi* A. Gray. These include an acaulescent growth habit, free stipules, basifixed pubescence, long, narrow flowers with barely incurved petals, and a bilocular legume. The finer details of the pod provide the best clues to the relatives of this species. Within section *Argophylli* is a group of four species (*A. waterfallii* Barneby, *A. feensis* M. E. Jones, *A. holmgreniorum* Barneby, and *A. eurylobus* Barneby), all of which have bilocular pods technically similar to those of *A. nutriosensis*. However, the shape, texture, and dehiscence of the bilocular pod in these four species is fundamentally different. Each is marked by a long, narrow, incurved pod, with trigonous or cordate cross-section (and sometimes incomplete septum), fleshy or ligneous valves, and dehiscence which is first apical, then through ventral and dorsal sutures. The pod of *A. nutriosensis* is short, broad, little incurved, terete in cross-section, completely bilocular, and pa-

pery in texture. Its dehiscence is unusual, involving separation of the pod into two closed halves, the seeds ultimately spilling through the septum walls.

The shape and texture of the pod are more similar to species in section *Mollissimi* A. Gray, particularly to *Astragalus mollissimus* vars. *thompsonae* (S. Wats.) Barneby and *matthewsii* (S. Wats.) Barneby, which are difficult to distinguish in the area of Nutrioso Creek. The dehiscence is similar to that of *A. anisus*, a narrow endemic of the Gunnison Valley, Colorado, of somewhat uncertain phylogenetic position [placed by Barneby in section *Argophylli* (Barneby 1964: 718), but by Jones in section *Mollissimi* (Jones 1923:230)]. Mature plants of *A. mollissimus* are typically much more robust than those of *A. nutriosensis*, but seedlings of the former may easily be confused with specimens of the latter if flowers or fruits are not present. The copious pubescence of *A. nutriosensis*, matched in *A. mollissimus*, contributes to the overall impression of similarity. The pod of var. *matthewsii* is completely bilocular, which, along with a tendency towards a dwarf habit, suggests that it may be the closest extant relative to *A. nutriosensis*.

Astragalus nutriosensis may be distinguished from *A. mollissimus* var. *matthewsii* by several characters: a much smaller pod, barely half the length of typical pods of species in the section; an almost sessile inflorescence with few flowers, which is unique in the section and rare among North American groups in general; and white flowers with barely recurved banners. These differ from the purple flowers and more reflexed banners characteristic of all other members of the section, except perhaps the recently rediscovered *Astragalus hartmanii* Rydb. from northern Chihuahua (Spellenberg pers. comm.; see e.g., Hartman 678, at NY) which is a robust, strongly caulescent, leafy plant otherwise quite dissimilar to *A. nutriosensis*.

Floral morphology. The flowers of *A. nutriosensis* are remarkably straight and narrow, even in the context of the long, narrow flowers typical of sections *Argophylli* and *Mollissimi*. In size and shape the white flowers resemble those of the distantly related section *Orophaca* (Torrey & A. Gray) Barneby and of *A. wittmannii* Barneby, of section *Humillimi* (M. E. Jones) Barneby. The flowers in both those cases are found on very short peduncles crowded together at the bases of the leaves (Barneby 1979). Perhaps this unusual syndrome represents convergent evolution for increasing flower number given the constraints of an inflorescence crowded among leaf-bases.

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NOTES

ADDITIONAL SUPPORT FOR THE RECENT-INVASIVE ADVENT OF MESQUITE (MIMOSA-CEAE: *Prosopis*) IN THE SAN JOAQUIN VALLEY, CALIFORNIA. — In a recent article (Holland, *Madroño* 34:324-333, 1987), I speculated that one or both species of mesquite present in the San Joaquin Valley (*Prosopis glandulosa* and *P. pubescens*) were naturalized sometime between 1870 and 1890. Additional support for the hypothesis of human-mediated establishment of *P. glandulosa* has since been found in an article by Mackie (*Nemophila* 8:30, 1920) from which we quote in part: "Some years ago, Mr. J. A. Jastro, a well-known cattleman, introduced the large-podded mesquite (*Prosopis glandulosa*) into the head of the San Joaquin Valley in Kern County to improve the cattle ranges. The bushes grew from seeds producing less than a dozen individuals. When these specimens fruited the cattle at once began to feed on the pods and in this manner the mesquite was spread over a large area lying between Buena Vista lake reservoir and Button Willow." Haas et al. (Texas Agric. Exp. Sta. Monogr. 1:10-19, 1973) have shown that *P. glandulosa* can produce flowers within three years of germination, although other information (Mooney et al., *In* Simpson, ed., *Mesquite: its biology in two desert scrub ecosystems*, 1977) indicates that longer periods may be normal. Given Linton's observation of "an occasional patch of mesquite and sage" on the north shore of Buena Vista Lake in 1907 (*Condor* 10:196-198, 1908), the introduction may have occurred as late as 1900.

Additionally, the statement in the first paragraph of my recent article (Holland, op. cit.) concerning the number and distribution of species of *Prosopis* is in error. According to Burkart and Simpson (*In* Simpson, op. cit.), the genus contains 44 species, 40 of which occur in the New World. — DAN C. HOLLAND, Dept. of Biology, Univ. Southwestern Louisiana, Lafayette 70504-2451 and BARRETT ANDERSON, Dept. of Botany, California Academy of Sciences, Golden Gate Park, San Francisco 94118. (Received 29 Mar 1988; revision accepted 12 Sep 1988.)

NEW COMBINATIONS IN *ARCTOSTAPHYLOS*
(ERICACEAE): ANNOTATED LIST OF
CHANGES IN STATUS

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ABSTRACT

A total of 53 names in *Arctostaphylos* are reviewed, 16 being synonyms. Of the remaining 37, designated hybrids account for 13 names: *A. × benitoensis* Roof, *A. × bracteata* T. J. Howell, *A. × cinerea* T. J. Howell, *A. × coloradensis* Rollins, *A. × helleri* Eastw., *A. × jepsonii* Eastw., *A. × laxiflora* Heller, *A. × oblongifolia* T. J. Howell, *A. × pacifica* Roof, *A. × parvifolia* T. J. Howell, *A. × strigosa* T. J. Howell (and also *A. × campbellae* Eastw. and *A. × media* Greene that had earlier achieved this status). Reductions from species to subspecies include 3 names: *A. sonomensis* Eastw., *A. montaraensis* Roof, and *A. knightii* Gankin & Hildreth; reductions from species to form comprise 5 names: *A. acutifolia* Eastw., *A. adenotricha* Löve, Löve & Kapoor, *A. candidissima* Eastw., *A. setosissima* Eastw., and *A. tracyi* Eastw.; and the remaining 16 names are downward shifts in infraspecific rank, mainly from variety to form.

Having studied the genus *Arctostaphylos* over a period of 30 years, I perceive difficulties for the non-specialist, but none greater than the numerous names existing at more than one, often vaguely defined, rank, mostly proposed at the species level, many of them synonyms or based on local forms or hybrid individuals. This paper deals mainly with reassignments in rank for validly published names that have escaped evaluation. A brief exposition of the logic guiding these taxonomic dispositions is essential. The taxonomic category variety has been used ambiguously in *Arctostaphylos*. It has been applied indiscriminately, on the one hand, to major geographic taxa with substantially allopatric distributions (that zoologists have long recognized as subspecies) and, on the other hand, to minor forms with locally sympatric or largely intrapopulational distributions (known to zoologists as morphs). There is a strong traditional usage of varietal rank in botany in lieu of subspecies, but the International Code recognizes variety as a rank intermediate between subspecies and form. Within *Arctostaphylos*, however, subspecies serves well as the category for variants of the species with more or less discrete geographic distributions, whereas form is the obvious choice for intrapopulational morphs (many species are dimorphic; e.g., hairy form/smooth form). Variety is then a superfluous category in the genus.

Examples of geographically discrete subspecies are well delineated in *A. hookeri*, *A. manzanita*, and *A. viscida* (Wells 1968) and more

complexly so in *A. glandulosa* and *A. tomentosa* (Wells 1987). Intrapopulational forms, based on minute indument characters, have received an inordinate amount of attention in the wide-ranging species, *A. uva-ursi*, predominantly in the northern part of North America and not in Eurasia. Comparable variation exists in the center of diversity for the genus in California, but the plethora of species and subspecies there inhibits the indulgence of naming all of the individual variation within populations; a beginning has been made in the relatively wide-ranging species, *A. glandulosa* (Wells 1987). The sympatric forms of *A. uva-ursi* include the following taxa named at the varietal or even subspecific level: var. *adenotricha* Fern. & Macbr., var. *coactilis* Fern. & Macbr., subsp. *longipilosa* Packer & Denford, subsp. *stipitata* Packer & Denford, and the nominate subsp. and var. *uva-ursi* in part of its North American range. In part because the pubescence forms serve as markers for ploidy level, many of them coexist in the same populations; *adenotricha* is diploid, *stipitata* and *uva-ursi* tetraploid, and *coactilis* and *longipilosa* variable (Packer and Denford 1974). On the other hand, the pubescence types intergrade and some phenotypic plasticity of indument in response to ecological factors has been observed (Rosatti 1987). The medley of intrapopulational variation within North American *A. uva-ursi* is most appropriately treated at the taxonomic level of form.

Another problem in *Arctostaphylos* is the occurrence of localized hybrid swarms or individuals at some points of sympatry for certain species. Unfortunately, some botanists with an eye for differences have collected hybrid individuals that later became the types of new taxa, invariably at the species level. A well known example is the group of taxa named at Waldo, Oregon, by T. J. Howell (1901). Waldo was a mining district of diverse lithology (serpentinite, conglomerate, sands, basalt-gabbro), much disturbed and open to invasion by manzanitas, chiefly *Arctostaphylos viscida* ssp. *pulchella* (on the serpentine) and *A. canescens* (on non-serpentine soils). The circumstantial evidence suggests the possibility of hybridization between these two species. Of the four Waldo taxa named as species by Howell, *A. bracteata* and *A. strigosa* are quite similar to *A. canescens* but differ slightly in the direction of *A. viscida*; the other two, *A. cinerea* and *A. oblongifolia*, are intermediate between *A. canescens* and *A. viscida*. Obvious hybrid swarms still existed at the Waldo site in the period 1960–1967, when I visited the area in search of Howell's taxa, but I was unable to discern any valid populations corresponding to his descriptions or to his specimens at Eugene (ORE). Fortunately, the populations of manzanitas at Waldo, as well as others in an area of several hundred square miles in southwestern Oregon, were analyzed biosystematically by Gottlieb (1968). Using hybrid index and scattered diagrams, Gottlieb quantitatively defined

the existence of hybrid swarms between *A. canescens* and *A. viscida* at Waldo and elsewhere in the surrounding region. He concluded that Howell's names were based on individual variants selected from hybrid swarms (Gottlieb 1968). In order to avoid arbitrary assignments to synonymy, as has been done with *A. bracteata* and *A. strigosa* under *A. canescens* by Adams (1940), reduction to hybrid status (e.g., *A. × bracteata* T. J. Howell) should suffice to neutralize the four superfluous names from the Waldo type locality. Proliferation of names for hybrid individuals (as done to excess in *Quercus*) should be avoided in *Arctostaphylos*, however. Only published names that already clutter the literature deserve this fate. Species of hybrid origin with substantial, stable populations (often ecologically isolated from the putative parental species) ought to be sustained as valid species; arbitrary use of hybrid designations for such well defined entities would wreak extensive havoc on the established taxonomy of the genus, inasmuch as the pattern of variation throughout *Arctostaphylos* is reticulate in nature.

ANNOTATED LIST OF PROPOSED CHANGES IN STATUS FOR
ARCTOSTAPHYLOS TAXA

- A. acutifolia* Eastw. See *A. patula* forma *acutifolia*.
A. adenotricha (Fern. & Macbr.) Löve, Löve & Kapoor. See *A. uva-ursi* forma *adenotricha*.
A. × benitoensis Roof (pro sp.), stat. nov. Basionym: *A. benitoensis* Roof, Four Seasons 5(4):5–8, 1978. This taxon appears to be *A. pungens* H.B.K.; introgressed with few traits of *A. glauca* Lindl. If *A. × benitoensis* constituted a coherent entity, it would be extremely close to *A. parryana* Lemmon, and might be placed in synonymy with that species.
A. bowermanae Roof, Four Seasons 5(4):15–18, 1978, from the north side of Mt. Diablo, is certainly *A. manzanita* Parry and possibly synonymous with subsp. *manzanita*.
A. × bracteata T. J. Howell (pro sp.), stat. nov. Basionym: *A. bracteata* T. J. Howell, Fl. N.W. Amer., 417, 1901. This is one of several hybrid intergrades between *A. canescens* Eastw. and *A. viscida* Parry (closer to the former), named as species by T. J. Howell, as elucidated by Gottlieb (1968) at the type locality near the site of Waldo, Oregon.
A. × campbellae Eastw. (pro sp.). Based on *A. campbellae* Eastw., Leaf. W. Bot. 1:75, 1933. Probably *A. tomentosa* (Pursh) Lindl. subsp. *crustacea* (Eastw.) Wells, slightly introgressed with few traits of *A. glauca* Lindl. (Wells 1987).
A. candidissima Eastw. See *A. canescens* forma *candidissima*.
A. canescens Eastw. subsp. **canescens** forma **candidissima** (Eastw.) Wells, comb. et stat. nov. Basionym: *A. candidissima* Eastw.,

Leaf. W. Bot. 3:124, 1942. A variably white-downy extreme form of *A. canescens* subsp. *canescens*.

- A. *canescens*** Eastw. subsp. ***sonomensis*** (Eastw.) Wells, comb. et stat. nov. Basionym: *A. sonomensis* Eastw., Leaf. W. Bot. 1:78, 1933. A consistently different glandular race of *A. canescens* with a wide but segregated (allopatric) distribution relative to the nominate subspecies (Knight 1985). Although subsp. *sonomensis* occurs on volcanic and other rocks, it appears to be restricted to serpentinite at the northern limits of its known range, as on the summit of Horse Mountain, Humboldt Co. (unpublished collection). Perhaps both glandulosity of pedicels and fruit and serpentine tolerance derive from some genes of *A. viscida* subsp. *pulchella* having introgressed into *A. canescens* subsp. *canescens* at some point in time and place.

- A. chaloneorum* Roof, Four Seasons 5(4):2-5, 1978, falls within the range of variation of *A. pungens* H.B.K. as does *A. benitoensis* Roof and *A. pseudopungens* Roof, all published in 1978. In this interlude of critical splitting, Roof departed from his prior course of lumping even distinct species such as *A. manzanita* Parry under *A. pungens* in an extraordinarily broad conception of the *A. pungens* "alliance" (Roof 1976). Later, he reduced *A. chaloneorum* as a subspecies under *A. pungens* (Roof 1979), a consistency that he did not extend to *A. benitoensis* and *A. pseudopungens*. Pending biosystematic elucidation of these populations, synonymy under *A. pungens* H.B.K. is appropriate for *A. chaloneorum* and *A. pseudopungens*.

- A. × *cinerea*** T. J. Howell (pro sp.), stat. nov. Basionym: *A. cinerea* T. J. Howell, Fl. N.W. Amer. 416, 1901. Another, more intermediate, individual variant in the well-known Waldo hybrid swarm, *A. canescens* × *A. viscida* (cf. Gottlieb 1968).

- A. × *coloradensis*** Rollins (pro sp.), stat. nov. Basionym: *A. coloradensis* Rollins, Rhodora 39:463, 1937. This name is based on intermediate individuals in the hybrid swarm *A. uva-ursi* × *A. patula* on the Uncompahgre Plateau of western Colorado. Remarkably, the same cross is taking place in northwestern Montana (ridge north of Lake Mary Ronan, Lake Co.; Lesica and Wells 1986) with some individuals matching *A. × coloradensis* (*A. patula* was previously unknown there, but *A. uva-ursi* is sympatric, being widespread in the Rocky Mountains). Other instances of this polytopic hybridization may come to light by surveying the wide distribution of *A. patula* forma *platyphylla*.

- A. *columbiana*** Piper forma ***setosissima*** (Eastw.) Wells, comb. et stat. nov. Basionym: *A. setosissima* Eastw., Leaf. W. Bot. 1:78, 1933. An intensely setose form of the variably hairy species that occurs locally with the nominate form, especially in southern Mendocino Co.

- A. columbiana** Piper forma **tracyi** (Eastw.) Wells, comb. et stat. nov.
Basionym: *A. tracyi* Eastw., Leafl. W. Bot. 1:79, 1933. A local form lacking setose hairs, except on the bracts (as on the type); all degrees of setosity can be found around Big Lagoon, Humboldt Co., the type locality of *A. tracyi*. Eastwood named it on the basis of the smooth-form specimens collected by Tracy. Both forma *tracyi* and forma *setosissima* occur as intrapopulational variants and should be treated as forms.
- A. edmundsii** J. T. Howell forma **parvifolia** (Roof) Wells, stat. nov.
Basionym: *A. edmundsii* var. *parvifolia* Roof, Leafl. W. Bot. 9: 191, 1961. A localized and intrapopulational, small-leaved form of possible horticultural value.
- A. glauca** Lindl. forma **eremicola** (Jeps.) Wells, stat. nov. Basionym: *A. glauca* var. *eremicola* Jeps., Madroño 1:78, 1922. This epithet is available for a decumbent form of *A. glauca* that layers; the spreading form occurs on the desert slopes of the Transverse and Peninsular Ranges. Layering from lower branches is a widespread trait in *Arctostaphylos*, however, and there is no need to formalize these vegetative forms by naming them unless, perhaps, there is horticultural potential.
- A. glauca** Lindl. forma **puberula** (J. T. Howell) Wells, stat. nov.
Basionym: *A. glauca* var. *puberula* J. T. Howell, Leafl. W. Bot. 2:70, 1938. This local variant in indument deserves a rank no higher than form.
- A. × helleri** Eastw. (pro sp.), stat. nov. Basionym: *A. helleri* Eastw., Leafl. W. Bot. 4:148, 1945. A putative hybrid, sympatric with both parents: *A. viscida* Parry × *A. myrtifolia* Parry on the Ione formation, a substratum to which the latter is narrowly endemic. Eastwood named it from an individual specimen collected by Heller (in *Arctostaphylos*, a treacherous undertaking). Surprisingly, this cross has escaped biosystematic attention, whereas the unnamed analogous cross, *A. viscida* × *A. nissenana* Merriam, has been well analyzed (Schmid et al. 1968).
- A. imbricata** Eastw. subsp. **montaraensis** (Roof) Wells, comb. et stat. nov. Basionym: *A. montaraensis* Roof, Four Seasons 2(3):6–16, 1967. Aside from its tall, erect habit, this taxon is similar to the creeping or mound-forming *A. imbricata* Eastw.; also, the nascent bracts differ subtly in shape, subsp. *montaraensis* having more acuminate tips. Although the differences are relatively minor, the main populations of the two taxa are segregated on two different mountains south of San Francisco, subsp. *imbricata* on San Bruno and subsp. *montaraensis* on Montara Mountain. At one spot on San Bruno, the two taxa coexist, indicating that they are genetically distinct (also shown in common gardens, as at Tilden); at San Bruno there are only a few individuals of subsp. *montaraensis* growing with a large population of subsp.

imbricata, whereas on Montara Mountain, closer to the Pacific coast, there are large populations of erect subsp. *montaraensis* but none of prostrate subsp. *imbricata*. The mainly allopatric distribution argues for a rank of subspecies.

A. intricata T. J. Howell, Fl. N.W. Amer., 416, 1901, is a later synonym for *A. glandulosa* Eastw. (1897); cf. Wells (1987).

A. × jepsonii Eastw. (pro sp.), stat. nov. Basionym: *A. jepsonii* Eastw., Leaf. W. Bot. 1:110, 1934. The existence of local hybrid zones between the elevationally segregated *A. patula* Greene and *A. viscida* subsp. *mariposa* (Dudley) Wells has been well documented (Epling 1947, Dobzhansky 1953). The earliest formal recognition of the intergradation was described as *A. mariposa* Dudley var. *bivisa* Jepson, Madroño 1:79, 1922. An appropriate name for the hybrid *A. patula* × *A. viscida* subsp. *mariposa* would be *A. × jepsonii* Eastw. because it honors the prior author and was proposed at the species level.

A. knightii Gankin & Hildreth. See *A. nevadensis* subsp. *knightii*.

A. × laxiflora Heller (pro sp.), stat. nov. Basionym: *A. laxiflora* Heller, Leaf. W. Bot. 4:148, 1945. This rare hybrid with very showy panicles stems from the putative cross *A. manzanita* Parry × *A. truei* W. Knight, the two most plausible parents near the type locality in Butte Co. on the lower slope of the Sierra Nevada.

A. manzanita Parry subsp. *bakeri* (Eastw.) Wells. Synonym for *A. bakeri* Eastw., which is now upheld as a distinct species.

A. × media Greene (pro sp.). Basionym: *A. media* Greene, Pittonia 2:171, 1891. The well known hybrid *A. uva-ursi* (L.) Spreng. × *A. columbiana* Piper has been studied most recently by Kruckeberg (1977). He has uncovered a parallel cross (*A. nevadensis* A. Gray × *A. columbiana*) that produces a phenotype similar to *A. × media* (as might be expected from the similarity of *A. nevadensis* and *A. uva-ursi*). Fortunately, no formal name has been proposed for this very similar hybrid.

A. montaraensis Roof. See *A. imbricata* subsp. *montaraensis*.

A. nevadensis A. Gray subsp. *knightii* (Gankin & Hildreth) Wells, comb. et stat. nov. Basionym: *A. knightii* Gankin & Hildreth, Four Seasons 3(3):23–24, 1970. My observations of this taxon in the field indicate a very close similarity to *A. nevadensis* A. Gray (and this is also apparent on the type specimen), except for variably developed lignotubers that are most consistently present at the type locality and nearby areas of Humboldt Co. In Del Norte Co., in the vicinity of Gasquet, there are extensive populations of *A. nevadensis* that mostly lack lignotubers; at Humboldt Flat in the hills above Gasquet, I noted as long ago as 1967 that some *A. nevadensis* had small basal burls, but attributed this to hybridization with sympatric *A. glandulosa*

Eastw. forma *cushingiana* (the latter as abundant as burl-free *A. nevadensis*). Since lack of consistency as to the presence of lignotubers is well known within other species of *Arctostaphylos* (e.g., *A. patula* Greene), an infraspecific rank is indicated. In view of the substantial allopatric populations in Humboldt Co., a rank of subspecies seems appropriate.

- A. nitens* Eastw., Leaflet. W. Bot. 4:149, 1945, appears from the type to be part of the *A. glandulosa* complex (Wells 1987), but along with other collections from southwestern Oregon deserves populational analysis in the field to determine consistency of the described traits, presence or absence of burls (uncertain), etc. Previous experience in this region indicates an extremely low probability of taxonomic significance for this name.
- A. × oblongifolia** T. J. Howell (pro sp.), stat. nov. Basionym: *A. oblongifolia* T. J. Howell, Fl. N.W. Amer. 416, 1901. Another name based on the hybrid swarm at Waldo, Oregon: *A. canescens* × *A. viscida*, and morphologically intermediate between the two parental species.
- A. obtusifolia* Piper, Bull. Torrey Bot. Club 29:642, 1902, is synonymous with *A. patula* forma *platyphylla* (A. Gray) Wells, q.v.
- A. × pacifica** Roof (pro sp.), stat. nov. Basionym: *A. pacifica* Roof, Leaflet. W. Bot. 9:217, 1962. Although it bears the stamp of an *A. uva-ursi* lineage, this tiny population on San Bruno Mountain has isofacial stomatal distribution and crown-sprouts from lignotubers. Past hybridization between *A. uva-ursi* (L.) Spreng. and *A. glandulosa* Eastw. is the putative ancestry, both parental species extant on San Bruno; non-sprouting forms of *A. uva-ursi* formerly grew near the putative hybrid but were locally eliminated by a relatively recent fire, while *A. × pacifica* resprouted under the observation of Knight, Raiche, Roof and others (see also the sprouting *A. uva-ursi* forma *suborbiculata*).
- A. parryana* Lemmon var. *pinetorum* (Rollins) Wiesel. & Schreieb. See *A. pinetorum*.
- A. × parvifolia** T. J. Howell (pro sp.), stat. nov. Basionym: *A. parvifolia* T. J. Howell, Fl. N.W. Amer. 416, 1901. Unlike the group of taxa named from the hybrid swarms at Waldo, *A. parvifolia* was based on collections from mountains west of Andersons, Oregon, a considerable distance north and west of Waldo. The type specimen has rather small green leaves, not gray as in the Waldo taxa, which are derived from the cross *A. viscida* (glaucous leaves) × *A. canescens* (gray, strigose-canescens leaves). The simple, racemose inflorescence and small, green leaves suggest that one parent was *A. nevadensis* A. Gray; the white-hairy ovary and pedicels could be derived either from *A. glandulosa* forma *cushingiana* (Eastw.) Wells or *A. canescens*.

Hybrid swarms of *A. nevadensis* × *A. glandulosa* and individuals resembling descriptions and type of *A. parvifolia* (with or without a burl) are still being generated at Humboldt Flat, Del Norte Co. On the other hand, Gottlieb (1968) decided that *A. parvifolia* stems from the same *A. viscida* cross as the Waldo hybrids.

- A. patula** Greene forma **acutifolia** (Eastw.) Wells, comb. et stat. nov. Basionym: *A. acutifolia* Eastw., Leafl. W. Bot. 3:125, 1942. A poorly known taxon, apparently collected only near the type locality, Log Springs Ridge in southwestern Tehama Co. Possibly, Eastwood named it as a counterpoint in leaf shape to *A. obtusifolia* Piper, a taxon that she accepted as a species (Eastwood 1934), even though the latter is indistinguishable morphologically from *A. patula* forma *platyphylla*. Examination of the type of *A. acutifolia* at CAS shows that it, too, is very close to *A. patula*, but differs in having glandular-hairy pedicels and stipitate-glandular fruit; the coalesced nutlets are seen also in *A. patula* forma *coalescens*, as described next.
- A. patula** Greene forma **coalescens** (W. Knight) Wells, stat. nov. Basionym: *A. patula* var. *coalescens* W. Knight, Four Seasons 7(1):20–21, 1984. The only distinguishing character is a tendency toward partial coalescence of the normally separable nutlets; coherence of nutlets occurs sporadically in the North Coast Range sector of the range of *A. patula* and may be expected elsewhere. Inasmuch as it has been formally named, it is retained as a form, but an occasional tendency toward coalescence of nutlets is a commonly observed variation in the genus, and ought not to be named; consistent fusion as a solid, indehiscent stone, on the other hand, is an excellent character.
- A. patula** Greene forma **platyphylla** (A. Gray) Wells, stat. nov. Basionym: *A. pungens* var. *platyphylla* A. Gray, Syn. Fl. N. Amer. 2:28, 1878; *A. patula* subsp. *platyphylla* (A. Gray) Wells, Madroño 19:203, 1968. Recent field studies indicate that many populations of *A. patula* commonly lack basal burls (lignotubers) in the northern part of the Sierra Nevada and in many parts of the North Coast Range, thus greatly reducing the allopatry of burl-forming *A. patula*. Since the greater part of the range of *A. patula*, from the northern Sierras and Cascades eastward disjunctly to the Rockies of Montana, Utah and Colorado and southward in Nevada, Arizona and Baja California, is occupied by populations that seem to *lack* the burl (forma *platyphylla*), attention should be focused on the actual extent of burl-forming populations (forma *patula*) in the Sierra Nevada and North Coast Range and whether there is segregation for the burl trait there. Considering that presence or absence of the burl

is the only distinguishing character and that this trait has not been well documented in the putative burl-forming populations, it seems best to recognize this difference as a form.

- A. pinetorum* Rollins, *Rhodora* 39:462, 1937, and *A. parryana* var. *pinetorum* (Rollins) Wiesel. & Schreiber, *Madroño* 5:46, 1939, are synonyms for *A. patula* forma *platyphylla*.
- A. pseudopungens* Roof, *Four Seasons* 5(4):9–11, 1978, is a misnomer because, like *A. chaloneorum* Roof, it is merely an outlying population of *A. pungens* H.B.K. It is apparent from the late James Roof's extensive writings (1978) that he misconceived *A. pungens* as being tetraploid on the basis of the somatic count ($2n=26$) reported in Munz (1959), when, in fact, it is mostly diploid, as is further confirmed by Niehaus' counts on *A. pseudopungens* ($n=13$), reported by Roof (1978). Neither *A. pseudopungens* nor *A. chaloneorum* are sufficiently different from *A. pungens* to require a formal name, though Roof is undoubtedly correct in his astute observation that both are introgressed (limitedly) by certain traits of *A. glauca* Lindl. The name *A. × benitoensis* Roof suffices to designate this introgression formally.
- A. pulchella* T. J. Howell, *Fl. N.W. Amer.* 416, 1901, is synonymous with *A. viscida* Parry subsp. *pulchella* (T. J. Howell) Wells, *Madroño* 19:204, 1968.
- A. serpentinicola* Roof, *Four Seasons* 5(4):12–15, 1978, is synonymous with *A. viscida* subsp. *pulchella* (T. J. Howell) Wells. In publishing this name, Roof (1978) neither justified the status of full species, distinct from *A. viscida* Parry, nor in any way distinguished *A. serpentinicola* from the prior name, *A. viscida* subsp. *pulchella*. In examining Howell's type of *A. pulchella*, Roof (1978:12) apparently did not observe that the pedicels are glandular-hispidulous and the ovaries stipitate-glandular, as was noted by me when I visited at ORE in 1967. Roof correctly noted that there are two fragments, one a sterile branch of *A. viscida*, the other a flowering branch that can be diagnosed, both obtained in mountains west of Andersons, Josephine Co., Oregon, April 1886 (T. J. Howell's handwriting). Finally, an affinity for serpentinite bedrock is also shown by the smooth-fruited *A. viscida* subsp. *viscida* of the Sierra Nevada, but it is not restricted to serpentinite, being widespread on the primarily granitic terrane. Thus, the correct name for the viscid-fruited, serpentiniticulous race of the North Coast Range and Siskiyou Mountains, north into southwestern Oregon, is *A. viscida* Parry subsp. *pulchella* (T. J. Howell) Wells.
- A. setosissima* Eastw. See *A. columbiana* forma *setosissima*.
- A. sonomensis* Eastw. See *A. canescens* subsp. *sonomensis*.
- A. stanfordiana* Parry forma *decumbens* Wells, stat. et nom. nov.

Basionym and holotype: as in *A. stanfordiana* var. *repens* Roof, Four Seasons 4(2):16–17, 1972. Because of the horticultural possibilities of this exceptionally beautiful species, this decumbent form deserves recognition. It should be noted that wherever manzanitas branch to the base, the lower branches layer (take root) if they contact the ground, so that there may be no end to the naming of decumbent forms in the genus. In this instance, the shrub is *not* repent or prostrate. Furthermore, the epithet *repens* should be avoided in this genus, as it has been used previously to designate another taxon, *A. × repens* (J. T. Howell) Wells, based on *A. cushingiana* Eastw. forma *repens* J. T. Howell (Leaf. W. Bot. 4:161, 1945).

- A. × **strigosa** T. J. Howell (pro sp.), stat. nov. Basionym: *A. strigosa* T. J. Howell, Fl. N.W. Amer. 417, 1901. Yet another name proposed by Howell for a variant closer to *A. canescens* in the hybrid swarm between the latter and *A. viscida* at Waldo, Oregon (cf. Gottlieb 1968).

A. tracyi Eastw. See *A. columbiana* forma *tracyi*.

- A. **uva-ursi** (L.) Spreng. forma **adenotricha** (Fern. & Macbr.) Wells, stat. nov. Basionym: *A. uva-ursi* var. *adenotricha* Fern. & Macbr., Rhodora 16:213, 1914. A largely intrapopulational, minutely glandular form, widely sympatric in northern North America and in the Rocky Mountains with nominate forma *uva-ursi*. The latter, eglandular form extends farthest north in the Arctic and has become circumboreal through Eurasia, where the species is relatively uniform and tetraploid ($n=26$). Counts on forma *adenotricha* have been consistently diploid (Packer and Denford 1974).

- A. **uva-ursi** (L.) Spreng. forma **coactilis** (Fern. & Macbr.) Wells, stat. nov. Basionym: *A. uva-ursi* var. *coactilis* Fern. & Macbr., Rhodora 16:212, 1914. Another intrapopulational form commonly present with forma *adenotricha* and forma *uva-ursi* in North America, differing from the former in being eglandular and from the latter in having the twigs and rachises minutely tomentulose; ploidy level is variable, mostly diploid. Forma *coactilis* alone extends south along the Pacific coast to California, where it encounters a number of other species of the genus, possibly giving rise to several local forms through hybridization. The named forms are listed below.

- A. **uva-ursi** (L.) Spreng. forma **leobreweri** (Roof) Wells, stat. nov. Basionym: *A. uva-ursi* var. *leobreweri* Roof, Changing Seasons 1(2):26, 1980. This is one of several slightly differing forms (two have been named) that occur as separate populations on San Bruno Mountain, just south of San Francisco; all but *leobreweri* (glabrescent twigs) have indument similar to forma *coactilis*, and are scarcely distinguished by leaf shape and habit. Forma

leobreweri has incipient lignotubers; it propagates clonally by suckering.

- A. uva-ursi** (L.) Spreng. forma **longipilosa** (Packer & Denford) Wells, stat. nov. Basionym: *A. uva-ursi* subsp. *longipilosa* Packer & Denford, Canad. J. Bot. 52:751, 1974. Yet another widely distributed intrapopulational form in North America, often sympatric with a number of other forms, especially forma *coactilis*, forma *adenotricha*, and forma *stipitata*. Both diploid and tetraploid counts were reported by the authors.
- A. uva-ursi** (L.) Spreng. forma **marinensis** (Roof) Wells, stat. nov. Basionym: *A. uva-ursi* var. *marinensis* Roof, Changing Seasons 1(2):19–21, 1980. A narrowly endemic, tetraploid form from Pt. Reyes ($n=26$, unpublished meiotic count). Reportedly has basal burl; may be sympatric with forma *coactilis* which is very similar, but forma *coactilis* lacks lignotubers.
- A. uva-ursi* (L.) Spreng. subsp. *monoensis* Roof, Changing Seasons 1(3):7–9, 1980, from the Sierra Nevada, is not significantly different in its minutely glandular indument from forma *adenotricha* and has a similar somatic number of $2n=26$ (diploid level, unpublished count by Wells on material from Tilden Botanical Garden, Berkeley). Closely resembles Rocky Mountain material of forma *adenotricha* (also diploid) and should be reduced to synonymy with it.
- A. uva-ursi** (L.) Spreng. forma **stipitata** (Packer & Denford) Wells, stat. nov. Basionym: *A. uva-ursi* subsp. *stipitata* Packer & Denford, Canad. J. Bot. 52:750, 1974. A consistently tetraploid form with indument solely of stipitate glands, but occurs as intrapopulational morph with forma *longipilosa*, forma *coactilis*, forma *adenotricha*, etc., only in the far west. None of this intrapopulational variation deserves recognition at a rank higher than form.
- A. uva-ursi** (L.) Spreng. forma **suborbiculata** (W. Knight) Wells, stat. nov. Basionym: *A. uva-ursi* var. *suborbiculata* W. Knight, Four Seasons 7(2):31–32, 1984. Another population from San Bruno Mountain, San Francisco that is known to horticulturists in the Bay Area by the sobriquet “miniature”, distinguished mainly by the rather round leaves and incipient lignotubers (documented crown-sprouter after recent fire; cf. *A. × pacifica*).

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ANNOUNCEMENTS

NEW PUBLICATIONS

HUMPHREY, R. R., *90 years and 535 miles: Vegetation changes along the Mexican border*, University of New Mexico Press, Albuquerque, New Mexico 87131, 1987, v, [i], 448 pp., illus., ISBN 0-8263-0945-3 (hardbound), price unknown. [A fascinating then-and-now photographic comparison of the 535 changing miles of vegetation along the 205 markers designating the U.S.-Mexican boundary from El Paso, Texas, to San Luis (by Yuma), Arizona; changes esp. evident in the Chihuahuan Desert, the semi-desert grassland, and the Sonoran Desert, with "no life-form or appreciable taxonomic changes along the largely ungrazed 60% of the boundary" east of El Paso (p. 430).]

MASON, C. T., JR. and P. B. MASON, *A handbook of Mexican roadside flora*, University of Arizona Press, 1615 E. Speedway, Tucson, Arizona 85719, 30 Oct 1987, [iv], 380 pp., illus., ISBN 0-8165-0997-2 (paperbound), \$19.95. [Some 200 taxa included.]

NOMENCLATURAL AND SYSTEMATIC REASSESSMENT OF
OPUNTIA ENGELMANNII AND *O. LINDHEIMERI*
(CACTACEAE)

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ABSTRACT

For more than 100 years the conspicuous, large prickly-pear of the Southwest was known as Engelmann Prickly-pear, *Opuntia engelmannii* Salm-Dyck. In 1965 Benson and Walkington placed the name in synonymy under *O. ficus-indica* (L.) Miller and proposed *O. phaeacantha* Engelm. var. *discata* (Griffiths) L. Benson and Walkington for the Engelmann Prickly-pear. Newly discovered morphological characters, especially a unique glochid arrangement within areoles, and restudy of the publication dates shows the correct name for the Engelmann Prickly-pear to be *Opuntia engelmannii* Salm-Dyck ex Engelm. Certain other taxa were found to share the glochid arrangement, in addition to other characters, warranting revised synonymy and the following new combinations: *O. engelmannii* var. *lindheimeri*; *O. engelmannii* var. *linguiformis*; *O. engelmannii* var. *flavispina*; and *O. engelmannii* var. *flexospina*.

RESUMEN

Por más de cien años el nopal grande y conspicuo del suroeste de los Estados Unidos ha sido conocido como "Engelmann Prickly-pear," *Opuntia engelmannii* Salm-Dyck. En el año 1965 Benson y Walkington reconocieron este nombre como sinónimo de *O. ficus-indica* (L.) Miller y propusieron para el "Engelmann Prickly-pear" el nombre *O. phaeacantha* Engelm. var. *discata* (Griffiths) L. Benson y Walkington. Caracteres morfológicos recientemente descubiertos, especialmente una distribución única de glóquidas adentro de las areolas, y un nuevo estudio de las fechas de publicación, muestra que el nombre correcto para el "Engelmann Prickly-pear" es *O. engelmannii* Salm-Dyck ex Engelm. Algunos otros taxa tienen en común con *O. engelmannii* la distribución de glóquidas y otros caracteres obligando a una revisión de sinonimia y a las combinaciones nuevas siguientes: *O. engelmannii* var. *lindheimeri*; *O. engelmannii* var. *linguiformis*; *O. engelmannii* var. *flavispina*; and *O. engelmannii* var. *flexospina*.

The Engelmann Prickly-pear was discovered by Wislizenus on his expedition through northern Chihuahua in 1846. Duplicate specimens were made available to Salm-Dyck and Engelmann. Engelmann's notes packaged on the lectotype read in part, "Original specimen . . . A shoot of this specimen was sent to Pr. Salm and described by him." Engelmann (1850) published his own description which differs significantly from that of Salm-Dyck (1850), under the name *Opuntia engelmannii* Salm-Dyck. Although Engelmann considered Salm-Dyck to be the author of the name (as "Salm. Mss."), his publication appeared in January 1850 (Stafleu and Cowan 1976), four months before Salm-Dyck's publication date (Salm-Dyck 1850,

Stafleu and Cowan 1985). Because Engelmann's paper has priority and because he attributed the name to Salm-Dyck, the correct full author citation of the name according to ICBN Art. 46.1, and Rec. 46E.1 (Voss et al. 1983) is *Opuntia engelmannii* Salm-Dyck ex Engelm.

The name, *O. engelmannii*, remained in wide usage for the conspicuous, large prickly-pear of the Southwest until 1965 when Benson and Walkington stated that the type represents a spiny individual ("*O. megacantha*") of the cultivated, usually spineless species, *O. ficus-indica* (L.) Miller. They placed *O. engelmannii* and *O. megacantha* Salm-Dyck in synonymy under *O. ficus-indica* and applied *O. phaeacantha* Engelm. var. *discata* (Griffiths) Benson and Walkington to the wild material, which continued to bear the common name, Engelmann Prickly-pear.

DISCUSSION

Upon examination of the morphological characters of *O. phaeacantha* var. *discata*, spiny and non-spiny forms of *O. ficus-indica*, and the lectotype of *O. engelmannii*, we discovered several characters apparently overlooked by Benson and Walkington. We found no significant differentiating morphological characters between the lectotype of *O. engelmannii* and *O. phaeacantha* var. *discata*; we consider them conspecific.

However, the following characters distinguish *O. engelmannii* from *O. ficus-indica*: areoles on pericarp 12–35 vs. 40–70; shrub habit vs. tree habit; glochids (within each areole on the middle of a stem-segment) conspicuous, 3–5 or more mm long, stout, of unequal lengths and widely spaced, generally throughout the areole (Fig. 1), vs. cryptic (even in spiny forms), less than 1.5 mm long, and in a tiny crescent near the apical margin of the areole (sometimes a few subapical, hidden in the wool) (e.g., McLeod 1255, OBI; Millspaugh 4523, NY; Stover 195, SD; Vanderwier s.n., OBI); and $2n=66$ ($2n=22$ for var. *cuija*) vs. $2n=88$ (Pinkava and McLeod 1971, Pinkava et al. 1973, Pinkava and Parfitt 1982). They cannot be distinguished on the basis of presence or absence of spines. Although spineless individuals of both species might have glochids reduced and inconspicuous, usually by removing the areole's tomentum the characteristic glochid pattern may be seen.

We do not agree with Benson and Walkington's interpretation that the type of *O. engelmannii* is from a cultivated plant. The label on lectotype reads: "hab. north of Chihuahua, common as high up as El Paso. 5–6 feet high. August 1846. A. Wislizenus, leg." A fruit packet reads: "largest species, North of Chihuahua, 5–6' high, also cultivated. Dr. Wislizenus, August 1846."

Britton and Rose (1919:148) wrote: "Salm-Dyck, who first studied

the species, doubtless had but a single specimen before him, and this or a duplicate is now in the herbarium of the Missouri Botanical Garden. This type specimen came from near Chihuahua City, from which place Dr. Rose has collected identical material. Dr. Engelmann, who published Salm-Dyck's name, described the plant as erect and 5–6 feet high, giving its range from Chihuahua City to Texas. These remarks of his were doubtless based on notes of Dr. Wislizenus, who collected the type and must have included more than one species; as Engelmann says it is both cultivated and wild, the cultivated plants doubtless referring to some of the many forms grown about towns and ranches." The lectotype specimen (MO) includes only a fruit and a half-stem-segment; there is no evidence that two species are included.

In regard to *O. ficus-indica*, Britton and Rose (1919:177–178) stated: "Dr. Griffiths has recently figured a reversion which appeared on the common spineless form which points very definitely to *O. megacantha* as the origin of this form." Benson (1982:517–518) wrote: "These two plants [*O. ficus-indica* and *O. megacantha*] were quite similar, and the evolutionary origin of those known as *O. ficus-indica* from those called *O. megacantha* (as the wild type) was postulated by David Griffiths (*Journal of Heredity* 5:222. 1914)." In fact, Griffiths (1914) did not mention *O. megacantha*. Benson (1982: 932) further stated: "This name [*O. engelmannii*] has been applied erroneously to the large conspicuous prickly-pear occurring from the deserts of California to those of Texas but the type is from a cultivated individual of the spiny '*Opuntia megacantha*' type." We interpret Wislizenus' note, "also cultivated," as saying that although he collected from a native (wild) plant of common distribution between northern Chihuahua and Texas, he also saw cultivated plants that, in his opinion, were of the same species.

Specimens collected in 1976 northeast of Ciudad Chihuahua (e.g., Mexico, Chihuahua, Rte 10, 2.4 mi e. of Buenaventura, 4950 ft elev., Pinkava et al. 13223, ASU 86565, 86566) very closely match the lectotype of *O. engelmannii*. These plants were neither under cultivation nor appear to have escaped; habit and young fruit were that of the wild Engelmann Prickly-pear, not that of *O. ficus-indica*. From photos, these plants are estimated to be from 4–5 feet tall and more or less erect; in cultivation, one might easily expect the native plants to grow to 5–6 feet. If the lectotype were from the cultivated spiny form of *O. ficus-indica* as proposed by Benson (1965, 1982), we would expect it to reach 10–12 or more feet in cultivation.

Therefore, we do not consider *O. engelmannii* as conspecific with *O. ficus-indica*. We are recognizing *O. ficus-indica* in the sense of Britton and Rose (1919) but including forms that differ only in the presence of spines.

Opuntia ficus-indica and *O. megacantha* have not been typified. *Opuntia megacantha*, known only from an inadequate description,

would require the selection of a neotype before this name could be applied to *O. ficus-indica*, which has priority. *Opuntia megacantha* predates *O. engelmannii* but until typified, *O. megacantha* plays no role in our decisions.

Opuntia lindheimeri Engelm. shares with *O. engelmannii* the glochid arrangement, fruit color, habit, "hairy" seedlings, and lack of red bases on yellow inner perianth segments (though some flowers have the perianth completely red, orange, etc.). There are relatively subtle differences between these taxa, warranting no more than varietal status for *O. lindheimeri*. In variety *lindheimeri* the chalky-white outer layer of the spines (as found in var. *engelmannii*) is absent or nearly so, allowing the translucent yellow core to be conspicuous, and the fruit is pyriform or rather abruptly narrowed at the base instead of barrel-shaped.

Opuntia engelmannii is distinguished from *O. phaeacantha* sensu stricto by the following characters: fruit internally red-purple vs. green; inner perianth segments completely yellow vs. yellow with red bases; taller habit; spines of seedlings long and hair-like; and glochids (within each areole on the middle of a stem-segment) stouter, of unequal lengths and widely spaced, generally throughout the areole (Fig. 1), vs. compacted into a dense crescent-shaped tuft at the apex of the areole and, at least in more mature areoles, a prominent columnar tuft near the center of the areole (Fig. 1). Although intermediate specimens occur, especially in some populations of Arizona, Nevada, and California, we recognize *O. phaeacantha* as distinct from *O. engelmannii*. We do not recognize varieties of the former.

The discovery of these suites of distinguishing characters necessitates recognition of *O. engelmannii* as a species distinct from *O. phaeacantha* and from *O. ficus-indica* but not specifically distinct from *O. lindheimeri*.

TAXONOMIC TREATMENT

OPUNTIA ENGELMANNII Salm-Dyck ex Engelm. in Engelm. & A. Gray, Boston J. Nat. Hist. 6:208. Jan 1850. Type: Mexico, Chihuahua, n. of Chihuahua, common as high up as El Paso. Aug 1846, *Wislizenus* 223 (Lectotype: MO 2015202! designated by Benson and Walkington [1965], photos ASU!, NY, POM).

Opuntia engelmannii Salm-Dyck, Cact. hort. dyck. 1849. Apr 1850. Illegitimate, later homonym (ICBN Art. 64). Type: duplicate material of type of *O. engelmannii* Salm-Dyck ex Engelm. None preserved (see Stafleu and Cowan, 1985).

1. *OPUNTIA ENGELMANNII* var. *ENGELMANNII*. Autonym created with the publication of *O. engelmannii* var. *cyclodes* Engelm. & Bigelow, Proc. Amer. Acad. Arts 3:291. 1856.

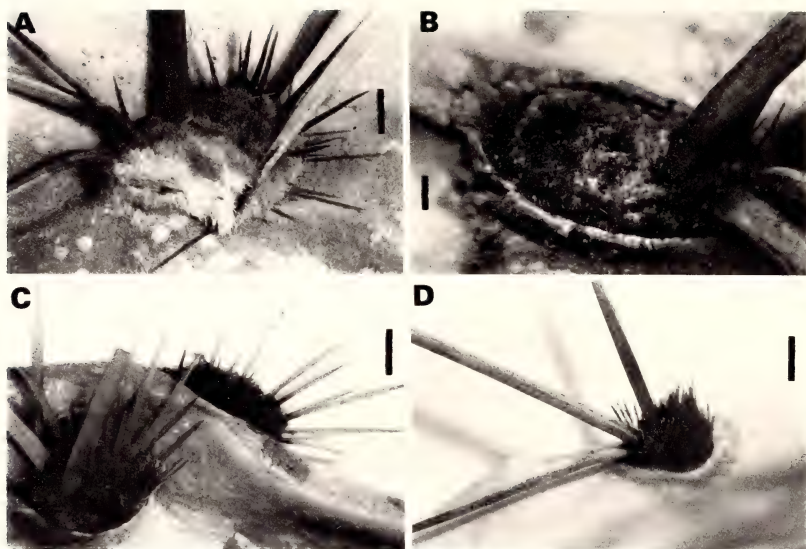


FIG. 1. Comparison of glochid arrangements of areoles midway between the base and apex of stem segments in four *Opuntia* taxa. A. *O. engelmannii* var. *engelmannii* (lectotype, Wislizenus 223, MO). B. *O. ficus-indica* (Stover 165, SD). C. *O. engelmannii* var. *lindheimeri* (topotype, Reeves 6333c sheet 2, ASU). D. *O. phaeacantha* (Worthington 10587, ASU). Scale line = 2 mm; placed at apical end of areole.

Opuntia discata Griffiths, Annual Rep. Missouri Bot. Gard. 19:265 + pl. 27 (upper fig.). 1908.—*O. engelmannii* Salm-Dyck var. *discata* C. Z. Nelson, Galesburg Republican Register, 20 Jul 1915; Trans. Illinois State Acad. Sci. 12:124. 1919.—*O. phaeacantha* Engelm. var. *discata* (Griffiths) L. Benson & Walkington, Ann. Missouri Bot. Gard. 52:265. 1965. Type: USA, AZ, foothills of the Santa Rita Mts, Apr 1905, Griffiths 7790 (Holotype: US 2572028A!, 2572029A!, 25720308A!, photos ASU!; isotype: POM 287144 [2 sheets]!, photos ASU!).

Opuntia dillei Griffiths, Annual Rep. Missouri Bot. Gard. 20:82–83 + pls. 2 (fig. 10), 4 (lower fig.), 13 (fig. 7). 1909. Type: USA, NM, San Andreas canyon of the Sacramento Mts, about 15 miles s. of Alamogordo, 3 Aug 1908, Griffiths 9460 (Holotype: US 2576308A!, 2576309A!, photos ASU!; isotype: POM 288128).

The names *O. engelmannii* and *O. lindheimeri* were simultaneously published (Engelmann 1850). Engelmann (1856) first treated the two as conspecific and placed *O. lindheimeri* into synonymy of *O. engelmannii*.

2. *Opuntia engelmannii* var. *lindheimeri* (Engelm.) Parfitt & Pinkava, comb. nov.—*O. lindheimeri* Engelm. in Engelm. & A.

Gray, Boston J. Nat. Hist. 6:207. Jan 1850.—*O. lindheimeri* Engelm. var. *lindheimeri*. Autonym created by Coulter (1896) with publication of *O. lindheimeri* var. *dulcis* (Engelm.) J. Coulter, var. *occidentalis* (Engelm. & Bigelow) J. Coulter, var. *cyclodes* (Engelm.) J. Coulter, and var. *littoralis* (Engelm.) J. Coulter. Type: USA, TX, New Braunfels, 1845, *Lindheimer s.n.* (Lectotype: MO 2016376! designated by Benson [1982], photo ASU!).

Opuntia lindheimeri Engelm. var. *lehmannii* L. Benson, Cact. Succ. J. (Los Angeles) 41:125. 1969. Type: USA, TX, Kleberg Co., King Ranch, 10 miles s. of ranch headquarters at Kingsville, 19 Apr 1965, *Lehman and Benson 16557* (Holotype: POM 317076! [4 sheets], photos ASU!).

Opuntia tricolor Griffiths, Annual Rep. Missouri Bot. Gard. 20:85–86 + pl. 4 (upper fig.). 1909.—*Opuntia lindheimeri* Engelm. var. *tricolor* (Griffiths) L. Benson, Cact. Succ. J. (Los Angeles) 41:125. 1969. Type: USA, TX, “prepared October 2, 1908, from cultivated specimens collected March 29, 1907, near Laredo,” *Griffiths 8651* (Holotype: US 2571220A!, photo ASU!; isotype: POM 287271; clonotypes: US 2571219A!, 2571221A!, photos ASU!).

Opuntia subarmata Griffiths, Ann. Rep. Missouri Bot. Gard. 20:94 + pls. 2 (fig. 1), 11, 13 (fig. 4). 1909.—[*O. engelmannii* Salm-Dyck var. *subarmata* Weniger, Cacti of the Southwest 180. 1970 (invalid name, ICBN Art. 33.2)].—*O. lindheimeri* Engelm. var. *subarmata* (Griffiths) Elizondo & Wehbe, Cact. Suc. Mex. 32: 16–18. 1987. Type: USA, TX, near Devils River, 22 Jul 1908, *Griffiths 9422* (Holotype: US 2572063A!, photo ASU!; isotype: POM 288607, 288608; clonotype: US 2572064A!, photo ASU!).

3. ***Opuntia engelmannii* var. *linguiformis*** (Griffiths) Parfitt & Pinkava, comb. nov.—*O. linguiformis* Griffiths, Annual Rep. Missouri Bot. Gard. 19:270. 1908.—*Opuntia lindheimeri* Engelm. var. *linguiformis* (Griffiths) L. Benson, Cact. Succ. J. (Los Angeles) 41:125. 1969.—[*Opuntia engelmannii* Salm-Dyck var. *linguiformis* (Griffiths) Weniger, Cacti of the Southwest 181. 1970 (invalid name, ICBN Art. 33.2)]. Type: USA, TX, near San Antonio, Aug 1906, *Griffiths 8377* (Holotype: US 2571222; isotypes: ASU 140761!, POM 317780).

[*Opuntia lindheimeri* Engelm. var. *brava* E. Schulz & Runyon, Trans. Texas Acad. Sci. 14:57. 1930 (invalid name, ICBN Art. 34.1a)]. For discussion of the name “var. *brava*,” see Benson (1969).

Variety *linguiformis* was considered by Schulz and Runyon (1930) to be a sterile mutant form. It is readily distinguishable by the lanceolate stem segments. In other characters it resembles var. *lindheimeri*. No native populations are known.

4. ***Opuntia engelmannii* var. *flavispina*** (L. Benson) Parfitt & Pinkava, comb. nov.—*O. phaeacantha* Engelm. var. *flavispina* L. Benson, Cact. Succ. J. (Los Angeles) 46:79. 1969. Type: USA, AZ, Pima Co., Organ Pipe Cactus National Monument, Ajo Mts, Alamo Canyon, 2300 ft, 27 Apr 1939, *Nichol s.n.* (Holotype: POM 306987; isotypes: ARIZ 64930, 83680; Herb. Organ Pipe Cactus Natl. Mon!; Herb. U.S. Natl. Park Service, Santa Fe).
5. **OPUNTIA ENGELMANNII** var. **CUIJA** Griffiths & Hare, New Mexico Agric. Exp. Sta. Bull. 60:44. 1906.—*Opuntia cuija* (Griffiths & Hare) Rose in Britton & Rose, Smithsonian Misc. Coll. 50:529. 1908.—*Opuntia lindheimeri* Engelm. var. *cuija* (Griffiths & Hare) L. Benson, Cact. Succ. J. (Los Angeles) 41:125. 1969. Type: Mexico, San Luis Potosi, *Griffiths 7596* (=7636) (Holotype: US 2576155A!, 2576156A!, photos ASU!; isotype: POM 287125).

Pinkava and Parfitt (1982) reported this taxon as diploid ($2n=22$). The remainder of *O. engelmannii* is hexaploid ($2n=66$). Although this taxon may be better treated as a species, we have chosen to treat it here pending resolution of the uncertainty regarding the application of *O. cantabrigiensis* Lynch, which has priority at the species level.
6. ***Opuntia engelmannii* var. *flexospina*** (Griffiths) Parfitt & Pinkava, comb. nov.—*O. flexospina* Griffiths, Bull. Torrey Bot. Club 43: 87. 1916.—[*O. engelmannii* Salm-Dyck var. *flexispina* [sic] (Griffiths) Weniger, Cacti of the Southwest 178. 1970 (invalid name, ICBN Art. 33.2)].—*O. strigil* Engelm. var. *flexospina* (Griffiths) L. Benson, Cact. Succ. J. (Los Angeles) 46:79. 1974. Type: USA, TX, vicinity of Laredo, dry gravelly hills, Jun 1911, *Griffiths 10301* (Holotype: US 2571224A!, 2571225A!, photos ASU!; isotypes: POM 299916, 290308).

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Reviews of the nomenclature by Edward G. Voss and Dan H. Nicolson are greatly appreciated. Allan D. Zimmerman provided helpful comments and discussion, especially regarding the Texas taxa. Sonia and Leslie Landrum kindly translated the abstract to Spanish. We thank the curators of ARIZ, ASU, MO, NY, OBI, POM, SD, US, and the herbarium of Organ Pipe Cactus National Monument for making specimens available for study.

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ANNOUNCEMENT

NEW PUBLICATIONS

FERREN, W. R., D. G. CAPRALIS, and D. HICKSON, 1987, *University of California, Santa Barbara, Campus Wetlands Management Plan. Part I, Technical Report on the Botanical Resources of West and Storke Campuses*. A Report to the UCSB Wetlands Committee. Environmental Research Team, The Herbarium, Department of Biological Sciences, University of California, Santa Barbara. Environmental Report No. 12. 198 pp. \$10.00. (Including Devereux Slough and portions of Goleta Slough.)

APT, K., C. D'ANTONIO, J. CRISP, and J. GAUVAIN, 1988. *Intertidal Macrophytes of Santa Cruz Island, California*. The Herbarium, Department of Biological Sciences, University of California, Santa Barbara. Publication No. 6. 87 pp. \$8.00.

Orders should be sent to The Herbarium, Department of Biological Sciences, University of California, Santa Barbara 93106. Checks should be payable to The UCSB Foundation.

SALIX SCOULERIANA (SALICACEAE) DISCOVERED IN MEXICO

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ABSTRACT

The boreal species *Salix scouleriana* has been found to occur in Mexico. A study of the type material of *Salix pattersonii* and *S. wendtii* revealed that both are *S. scouleriana*. The original identification of *S. wendtii* as new was due, in part, to a misunderstanding of the change that occurs in ament morphology when a plant flowers twice in the same year.

RESUMEN

La especie boreal *Salix scouleriana* se ha encontrado en México. Un estudio de *Salix pattersonii* y de *S. wendtii* ha descubierto que ambas especies son *S. scouleriana*. La identificación original de *S. wendtii* como especie nueva se debe, en parte, a un mal entendimiento del cambio que ocurre en la morfología del amento cuando una planta produce sus flores dos veces durante el mismo año.

The genus *Salix* is less well known in Mexico than it is in other parts of North America. Since C. Schneider's 1918 conspectus of the genus in Mexico, West Indies, and Central and South America only five papers on the genus in this region are known to me (Standley 1920, Johnston 1944, Espinosa 1979, Johnston 1981, Nee 1984). In the southwestern United States there are about eight willows of arctic-alpine (*S. arctica* Pall., *S. brachycarpa* Nutt., *S. glauca* L., *S. reticulata* ssp. *nivalis* (Hook.) A. Löve, D. Löve & Kapoor) or boreal (*S. bebbiana* Sarg., *S. drummondiana* J. Barratt ex Hook., *S. planifolia* Pursh, *S. scouleriana* J. Barratt ex Hook.) affinities that occur at relatively high elevations. None of these species have been reported to occur in Mexico, although suitable habitats, at least for some of the boreal species, are to be found there. It did not come as a complete surprise, therefore, to find one of them present in Mexico under a different name.

In the course of studying the holotypes of two Mexican *Salix*, *S. pattersonii* M. C. Johnston and *S. wendtii* M. C. Johnston, I discovered that both are the widespread boreal species *S. scouleriana*, a species not previously known to occur in Mexico. Both of Johnston's new species, which were described in 1981, were based on single collections: *S. pattersonii* on *Riskind and Patterson 1809* (LL) and *S. wendtii* on *Wendt and Adamcewicz 518* (TEX). In addition

to the holotypes two specimens tentatively identified as *S. pattersonii*, namely, *Wendt 124a* (TEX), and *Riskind et al. 1720* (LL) and two specimens listed as "*Salix* sp. nov.?", *Wendt and Lott P29* (CAN, TEX) and *Mueller 3242* (LL), have also been identified here as *S. scouleriana*.

The Mexican specimens have the following characteristics that are typical of *S. scouleriana* (Argus 1973): (1) Large floral winter buds; (2) leaves with two kinds of indumentum, (a) leaves sparsely pubescent beneath with a mixture of white and ferruginous hairs, and (b) leaves densely tomentose beneath with white hairs, but with a few ferruginous hairs on the upper surface; (3) aments usually sessile, or borne on a short spur shoot and usually flowering precociously (see below); (4) pistils sericeous with a mixture of ferruginous and white hairs; (5) pistils borne on long stipes (1.2–2.4 mm); and (6) black or dark brown floral bracts.

The holotype of *S. wendtii* is an apparent exception to character (3) in that its aments are borne on long, leafy shoots and are flowering in early August. Precocious species flower before the leaves appear and have sessile aments, whereas coetaneous and serotinous species flower with or after leaf emergence and have aments borne on prominent leafy spur shoots. This distinction between precocious and coetaneous and serotinous species is usually given high taxonomic value in the identification of *Salix*. The presence of an exceptionally long spur shoot in this holotype is most likely what directed Johnston's attention away from *S. scouleriana* or any of the other precociously flowering species. A close examination, however, reveals that the aments on this plant emerged from buds formed that year and therefore represent a second flowering. In some precociously flowering species aments that emerge from buds in the same year in which they were formed are borne on long, leafy shoots rather than being sessile. This condition was observed previously in *S. planifolia* in northern Saskatchewan (Argus 1979). In that particular case, as well, the plants were described as a new species, *S. tyrrellii* Raup, and incorrectly aligned with *S. glauca* before being correctly recognized as *S. planifolia*. In addition to having aments borne on long, leafy spur shoots, plants that flower twice in the same year also tend to have more prominent stipules—possibly a reflection of their vigorous growth. During field work in Arizona in 1986 I found a specimen of *S. scouleriana* exhibiting second flowering and very vigorous growth (*Argus and Argus 12383* CAN), so the condition displayed by the type of *S. wendtii* was familiar to me.

The Mexican specimens of *S. scouleriana* tend to differ from northern specimens in having more villous or shaggy branchlets. The species usually has short, velutinous hairs on young branchlets, but some variation in branchlet indumentum does occur in the species. It is not surprising, in any case, that these isolated, disjunct

populations in the Southwest diverge somewhat from the main species populations.

Salix scouleriana occurs in western boreal North America (Little 1976, map 179) from Alaska eastward to Manitoba and southward in the cordillera to southern California, Arizona, and New Mexico. The Mexican specimens of *S. scouleriana* known so far are all from Coahuila, two from Sierra Maderas del Carmen, Mpio. de Ocampo and two from Sierra de la Madera, Cañon de Agua.

The habitat of *S. scouleriana* in the southwestern United States, where it usually occurs as scattered individuals, is in mixed conifer forests on steep, relatively dry slopes at elevations of 2350 to 3000 m.

Salix scouleriana in Mexico is similar morphologically and ecologically to the populations of the species in adjacent New Mexico and Arizona. Its Mexican occurrence is significantly disjunct from known localities in northern Arizona and New Mexico, but not unexpected. A thorough field study of Mexican *Salix* could be expected to extend the range of this boreal-cordilleran species even further and perhaps even to find other species of northern affinities.

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NOTEWORTHY COLLECTIONS

CALIFORNIA

MUHLENBERGIA APPRESSA C. O. Goodding (POACEAE).—Los Angeles Co., San Clemente Island: 26 Apr 1912, *Wootton s.n.* (US); canyon below the Tomb, w. side of island, 148 m, 12 Apr 1962, *Raven 17324* (RSA); second canyon s. of Seal Cove, 33 m, 8 May 1962, *Raven 17603* (RSA); road just n. of Guds, 270 m, 9 May 1962, *Raven 17651* (RSA); canyon just n. of Gray, 460 m, 9 May 1962, *Raven 17708* (RSA); middle portion of Norton Canyon, 295 m, 11 Apr 1973, *Thorne 42857* (RSA, NY). San Bernardino Co., Providence Mts.: rocky slopes, 1476 m, 17 May 1930, *Hoffman 18* (US); canyon above Bonanza King Mine, 1509 m, 29 Oct 1977, *Thorne, Tilforth, and Prigge 50701* (RSA).

Previous knowledge. Known only from s.c. AZ and Baja California, Mexico where it generally occurs above 1300 m. Closest known station to San Clemente Island is 280 km se. near Santa Catarina, Sierra de Juarez, Baja California (1962, *Broder 708*, ARIZ, MEXU). Closest known station to the Providence Mts. is 350 km e. at Camp Creek Divide, Maricopa Co., AZ (1970, *Parker s.n.*, ARIZ).

Significance. New records for CA and the California Channel Islands.

This species is closely related to *M. microsperma* (DC.) Kunth and can be distinguished by its basally broadened and longer (4.0–6.2 mm) lemmas, longer glumes (1.0–2.0 mm), and by its narrow, ascending, loosely flowered panicle with closely appressed branches. The specimens from San Clemente Island tend to have slightly more open panicles than the type (*Harrison and Kearney 1493*, US) but match in all other characteristics.

MUHLENBERGIA FRAGILIS Swallen (POACEAE).—San Bernardino Co., Clark Mt. Range, gravelly limestone soil in wash, below corral near Pacific Mine, T17N R57E, 1570 m, 9 Oct 1977, *Prigge 2214* (RSA).

Significance. First record for CA, a range extension of ca. 475 km n. and nw. from previously known locations in Sierra Juarez, Baja California, Mexico, and Gila Co., AZ.

MUHLENBERGIA PAUCIFLORA Buckl. (POACEAE).—San Bernardino Co., New York Mts., upper Caruthers Canyon, sandy loam soils with *Pinus monophylla* Torr. & Frem., *Quercus turbinella* Greene, and *Garrya flavescens* Wats., T14N R16E S31 se.¼, 1755 m, 11 Sep 1983, *Peterson, Annable, and Barkworth 1622* (UNLV, WS).

Significance. First record for CA, a range extension of ca. 200 km w. from previously known locations in Yavapai Co., AZ.—PAUL M. PETERSON and CAROL R. ANNABLE, Dept. of Botany and Ownbey Herbarium, Washington State Univ., Pullman, 99164.

COLORADO

ASPENIUM SEPTENTRIONALE (L.) Hoffm. (ASPENIACEAE).—Moffat Co., Dinosaur National Monument, Douglas Mountain, 1.6 air km ne. of Zenobia Peak, on red sandstone outcrops and knolls of the Uinta Mountain Group, with *Pinus ponderosa* and *Cercocarpus ledifolius*, T8N R102W S28, 2560 m, 28 Jun 1987, *Neely 4455* (COLO, CS, Dinosaur N. M.).

Significance. This collection represents a range extension of ca. 52 km from the nearest location in Uintah Co., UT. Known elsewhere in w. CO only from Box Canyon, Ouray Co., 305 km to the se. (Weber, *Colorado Flora: Western Slope*, CO Assoc. Univ. Press, 1987).

ASTRAGALUS HAMILTONII C. L. Porter (FABACEAE).—Moffat Co., Dinosaur National Monument, hills west of Deerlodge Park, in sandy interstices of small barren outcrops

of the Morrison Formation with *Juniperus* and *Cercocarpus intricatus*, T6N R99W S28, 1756 m, 17 May 1987, *O'Kane 2768* (COLO, Dinosaur N. M.).

Significance. First CO record of this candidate for Threatened or Endangered status. This collection represents a range extension of ca. 62 km ne. of the nearest population 16 km north of Bonanza in Uintah Co., UT. The few other populations occur in nw. Uintah Co. at 1580 to 1935 m on soil derived from the Duchesne River Formation (Welsh & Chatterly, *Great Basin Naturalist* 45:173–236, 1985).

ENCELIOPSIS NUDICAULIS (Gray) A. Nels. (ASTERACEAE).—Moffat Co., Dinosaur National Monument, Yampa Bench, between the Billiard Table and Mantle Ranch Road, 2.4 km n. of Red Rock Ranch, Park City Formation, on heavy clay hills with *Atriplex confertifolia*, *Tetradymia spinosa*, and *Machaeranthera grindelioides*, T6N R103W S10, 1720 m, 30 May 1987, *Neely 4131* (CS, COLO, Dinosaur N. M.); Dinosaur National Monument, Mantle Ranch Road where it crosses Red Rock Canyon, Park City Formation, T6N R103W S11, 1691 m, 2 Jun 1987, *O'Kane 3035* (COLO, CS, Dinosaur N. M.).

Significance. First CO records and representing a range extension of ca. 32 km from near the Green River in Uintah Co., UT. The species is scattered across the Great Basin, Mohave Desert, Uinta Basin and Colorado Plateau in UT, NV, AZ and CA (Welsh, *In* Welsh et al., *Great Basin Nat. Mem.* 9:1–894, 1987) and is disjunct along the Salmon and Lemhi rivers in ID (Hitchcock and Cronquist, *Flora of the Pacific Northwest*, Univ. Wash. Press, 1973).

ZIGADENUS VAGINATUS (Rydb.) Macbr. (LILIACEAE).—Moffat Co.: Dinosaur National Monument, Blind Canyon, s. tributary of Yampa River, ca. 0.8 km n. of Mantle Ranch Road, in deep overhanging alcove with *Aquilegia micrantha* and *Cirsium ownbeyi*, T6N R102W S23, 1762 m, 2 Jun 1987, *O'Kane 3037* (COLO, CS, Dinosaur N. M.).

Significance. These collections are the first reports of this species from Colorado. It is infrequently found in Dinosaur National Monument where it grows in hanging gardens of alcoves with *Aquilegia micrantha* and, occasionally, with the narrowly endemic *Cirsium ownbeyi*. Populations in CO are disjunct by ca. 210 km from the nearest location in Grand Co., UT. A few other populations are found in Kane and San Pete Cos., UT (Welsh, *In* Welsh et al., *Great Basin Nat. Mem.* 9:1–894, 1987). A collection from e. of Echo Park Campground in the Monument (N. Holmgren in 1961, UTC) also is referable to this species (L. Schultz pers. comm.).

The field work leading to this report was supported by the National Park Service under a contract with the Colorado Department of Natural Resources.—STEVE L. O'KANE, JR., Dept. Biology, Box 1137, Washington Univ., St. Louis, MO 63130; ELIZABETH E. NEELY, The Nature Conservancy, 1244 Pine St., Boulder, CO 80302; and DIETER H. WILKEN, Dept. Biology, Colorado State Univ., Ft. Collins, CO 80523.

IDAHO

CARDAMINE CONSTANCEI Detling (BRASSICACEAE).—Shoshone Co., hillsides, 1.6 km w. of Kellogg, 15 Jun 1929, *Geo. G. Hedgcock s.n.* (WIS); on slope, 6.4 km se. of Kellogg, 15 Jun 1929, *Geo. G. Hedgcock s.n.* (WIS).

Previous knowledge. *Cardamine constancei* was first applied to specimens collected 2 Jun 1935 from Three Devils Creek, a tributary of the Middle Fork of the Clearwater River, Selway National Forest (Clearwater National Forest), Idaho County, Idaho. Greatest numbers of this formerly threatened, rare, endemic species occur under *Thuja plicata* Donn ex D. Don forests at lower elevations within the coast-like refugium, lower Selway River and nearby portions of the Middle Fork of the Clearwater River, that house other Idaho endemics and disjunct coastal vegetation. Smaller populations exist outside this optimum environment along the lower St. Joe, South Fork of the Coeur d'Alene (Pine Cr.), and the North and South Forks of the Clearwater

River in Clearwater, Idaho, Nez Perce, and Shoshone counties (Henderson et al., For., Wildlife, Range Exp. Sta. Bull. 21. Univ. Idaho, Moscow, 1977; and Crawford, M.S. thesis, Univ. of Idaho, Moscow, 1980). A collection from along Jackass Cr., a tributary of the w. fork of Pine Cr., and from the w. fork of Pine Cr., 9.7 and 6.4 km s. of Pinehurst made 31 May 1950 by J. H. and C. B. Christ, 19295 and 19279 respectively, are the only previous records of this species from northern Shoshone County.

Significance. The Hedgcock collections, located 10.3 and 15.3 km by air northeast of the northernmost Pinehurst collection, document a second location for the rare "State Watch" species, *Cardamine constancei*, in northern Shoshone County, Idaho and extend its northern limit 7.1 km. Additionally, Hedgcock's collections, discovered among the exsiccatae purchased by WIS in 1985 from LCU, predate the type collection and may be the first gatherings of this rare Idaho endemic. Mining and road building activities have modified the landscape in and around Kellogg since Hedgcock's visit and his collection sites may no longer exist. Tributaries of the South Fork of the Coeur d'Alene River in the vicinity of Kellogg could house as yet undiscovered populations of this rare *Cardamine*.—CLARK G. SCHAACK, Dept. of Botany, Univ. of Wisconsin, Madison 53706 and DOUGLASS M. HENDERSON, Dept. of Biological Sciences, Univ. of Idaho, Moscow 83843.

MONTANA

ASTRAGALUS CICER L. (FABACEAE).—Lake Co., foothills of the Swan Range ca. 5 km se. of the town of Swan Lake, T25N R17W S30, abundant in disturbed soil along a logging road, 1160 m, 1 Sep 1987, *P. Lesica 4505* (MONTU, NY) (verified by R. Barneby, NY).

Significance. First report of this Eurasian species for MT.

BARBAREA VULGARIS R. Br. (BRASSICACEAE).—Flathead Co., Glacier National Park, horse pasture near the Quarter Circle Bridge on McDonald Creek ca. 2 km w. of Park Headquarters, common in disturbed soil, 945 m, 3 Jun 1986, *P. Lesica and A. DeBolt 3759* (MONTU); Lincoln Co., less than 1 km se. of Idaho border and 25 km nw. of Troy, T34N R34W S32 nw.¼, many flowering plants in lush, moist meadow on the bank of Curley Creek, 755 m, 3 Jun 1987, *K. H. Lackschewitz 11232* (ID, MONTU, NY); Missoula Co., vicinity of Ninemile Ranger Station, 10 km ne. of Alberton, T15N R22W S8, frequent in a cleared pasture, 965 m, 7 Jun 1966, *J. Christensen and D. Owen s.n.* (RM); Kelly Island Fishing Access, 8 km w. of Missoula, T13N R20W S22 s.½, moist meadow along Clark Fork River, 975 m, 22 Jun 1987, *K. H. Lackschewitz 11256* (MONTU, NY) (*Lackschewitz 11232* and *11256* verified by A. Cronquist, NY).

Significance. First records of this Eurasian species for MT.

CAREX EBURNEA BOOTT (CYPERACEAE).—Dawson Co., head of North Fork of Burns Creek ca. 40 km nw. of Glendive, T21N R55E S19, locally common in hardwood forest on a moderate n.-facing slope, 900 m, 11 Jun 1987, *P. Lesica 4290* (MONTU, NY); Fergus Co., foothills of the Big Snowy Mtns. along Rock Creek ca. 24 km sw. of Lewistown, T13N R17E S25 se.¼, locally common in moist spruce forest on gravelly limestone soil, 1555 m, 17 Jun 1987, *P. Lesica 4321* (MONTU); Flathead Co., foothills of the Whitefish Range ca. 2 km ne. of Whitefish, T31N R21W S29 nw.¼, uncommon in moist spruce forest, 915 m, 21 Jul 1987, *P. Lesica 4429* (MONTU, NY) (*Lesica 4290* and *4429* verified by A. Cronquist, NY).

Significance. Although reported for MT by Kolstadt (Great Plains Flora Association, Flora of the Great Plains, 1986), these are the first confirmed records. The Flathead Co. collection is the first record for the Pacific Northwest and a range extension of ca. 400 km s. from Alberta. The Dawson Co. collection is a range extension of ca. 120 km nw. from Billings Co., ND.

CAREX TENUIFLORA Wahl. (CYPERACEAE).—Flathead Co., Glacier National Park, Numa Ridge ca. 3 km ne. of the foot of Bowman Lake ca. 10 km ne. of Polebridge, common on hummocks of a *Sphagnum* bog, 1525 m, 24 Aug 1987, *P. Lesica* and *A. DeBolt* 4106 (MONTU, NY) (verified by A. Cronquist, NY).

Significance. First report for MT and the Pacific Northwest, a range extension of ca. 400 km s. from Alberta.

CYTISUS SCOPARIUS (L.) Link (FABACEAE).—Sanders Co., n. above Hwy 200 between Hwy 56 and the Heron turnoff, T26N R33W S30, many plants for ca. 300 m in the roadcut and on the partially disturbed slope along the highway, 705 m, 4 Jun 1987, *K. H. Lackschewitz* 11245 (ID, MONTU, NY) (verified by A. Cronquist, NY and D. Henderson, ID).

Significance. First report of this Eurasian species for MT.

GENTIANOPSIS SIMPLEX (A. Gray) Iltis [= *Gentiana simplex* A. Gray] (GENTIANACEAE).—Missoula Co., Granite Creek, 4.8 km wsw. of Lolo Hot Springs, 0.16 km e. of Lolo National Forest Rd. 9942, ca. 3 km s. of jct. with Rd. 4209, T11N R24W S15 ne.¼ of se.¼, ca. 80–100 plants, growing in small clusters on hummocks in a spring seep area along the creek, 1360 m, 19 Jul 1986, *J. S. Shelly* and *G. V. King* 1231 (WIS); same location ca. 100–150 plants, 20 Jul 1987, *J. S. Shelly*, *K. H. Lackschewitz*, and *J. H. Rumely* 1377 (MONTU); same location, locally abundant, on raised margins and interfluvies of braided creek meanderings, substrate muddy, appearing marly, 20 Jul 1987, *J. H. Rumely*, *J. S. Shelly* and *K. H. Lackschewitz* 20/VII/87-04 (MONT).

Significance. First records for MT, a range extension of ca. 280 km from central ID. Also known from CA, OR, and NV.

HELENIUM HOOPESII A. Gray [= *DUGALDIA HOOPESII* (A. Gray) Rydb.] (ASTERACEAE).—Beaverhead Co., ca. 0.5 km e. of Monida, T14S R6W S35 sw.¼, in boggy area below the road to Red Rock Lakes, 2040 m, 1 Aug 1986, *K. H. Lackschewitz* 11061 (MONTU, NY) (verified by A. Cronquist, NY).

Significance. Although previously reported for MT by Davis (Flora of Idaho, 1952), no MT records were cited by Bierner (Brittonia 26:385–392, 1974). This is the first confirmed report. This species becomes more common just south in adjacent Clark Co., ID.

HUTCHINSIA PROCUMBENS (L.) Desv. (BRASSICACEAE).—Beaverhead Co., Armstead, dry saline soil among grass, 1675 m., 20 Jun 1920, *E. B. Payson* and *L. B. Payson* 1729 (RM); Tendoy Mtns., n. side of upper Big Sheep Creek Canyon 20 km sw. of Lima, T15S R10W S10, locally common beneath sagebrush on a steep, w.-facing, limestone talus slope, 2090 m, 13 Jun 1986, *P. Lesica* 3834 (GH, MONTU) (*Lesica* 3834 verified by R. Rollins, GH).

Significance. First records for MT. Reed Rollins (personal communication) believes that the correct name for this species is *Hymenolobus procumbens* (L.) Nutt. ex Torr. and A. Gray.

LINARIA CANADENSIS (L.) Dum. var. *TEXANA* (Scheele) Penn. (SCROPHULARIACEAE).—Dawson Co., Makoshika State Park just e. of Glendive, T15N R56E S32, disturbed grassland, 635 m, 30 Jun 1982, *K. Scow*, *D. Culwell* and *L. Larson* s.n. (MONTU); Carter Co., low ridge ca. 8 km sw. of Alzada, T9S R59E S31, common in open, sandy soil of a pine-oak woodland, 1125 m, 15 Jun 1986, *P. Lesica* 4124 (MONTU, NY) (*Lesica* 4124 verified by A. Cronquist, NY).

Significance. First records for MT. The Carter Co. collection is a range extension of ca. 32 km nw. from Crook Co., WY; the Dawson Co. record is a range extension of ca. 280 km nw. from Grant Co., ND.

LYCHNIS FLOS-CUCULI L. (CARYOPHYLLACEAE).—Lincoln Co., less than 1 km se. of Idaho border and 25 km nw. of Troy, T34N R34W S32 nw.¼, 50–60 plants in a moist meadow on the w. bank of Curley Creek, 755 m, 3 Jun 1987, *K. H. Lackschewitz 11233* (ID, MONTU, NY) (verified by A. Cronquist, NY and D. Henderson, ID).
Significance. First report of this Eurasian species for MT.

MYOSOTIS DISCOLOR Pers. (BORAGINACEAE).—Sanders Co., Beaver Gulch Rd., 5 km w. of Heron, T26N R34W S5 e.½, in drying vernal pools, 680 m, 4 Jun 1987, *K. H. Lackschewitz 11239* (ID, MONTU, NY) (verified by A. Cronquist, NY and D. Henderson, ID).

Significance. First report of this Eurasian species for MT.

POLYSTICHUM SCOPULINUM (D. C. Eat.) Maxon (POLYPODIACEAE).—Sanders Co., Cabinet Gorge, w. bank of the Clark Fork River 4.8 km nw. of Noxon, T26N R33W S23 n.½, one large plant in lichen-covered rocks of old riprap just above the water line, 665 m, 24 Jun 1986, *K. H. Lackschewitz 10915* (MONTU, NY) (verified by A. Cronquist, NY).

Significance. Second report for MT. The occurrence of this species in a man-made, low elevation habitat is unusual.

RIBES COGNATUM E. Greene (GROSSULARIACEAE).—Sanders Co., Cabinet Gorge, w. bank of Clark Fork River 3 km nw. of Noxon, T26N R33W S23 n.½, in a relatively dry site at the foot of exposed cliffs, 675 m, 24 Jun 1986, *K. H. Lackschewitz 10919* (MONTU, NY) (verified by A. Cronquist, NY); Lincoln Co., above Yaak River Falls 20 km n. of Troy, T33N R33W S5 se.¼, in dry cliffs, 730 m, 26 Jun 1986, *K. H. Lackschewitz 10934* (MONTU, NY); along Kootenai River above Kootenai Falls 10 km e. of Troy, T31N R32W S13, one plant in cliffs, 620 m, 2 Jun 1987, *K. H. Lackschewitz 11220* (ID, MONTU) (verified by D. Henderson, ID).

Significance. First records for MT, an extension of 40 km east from Bonner Co., ID.

SATUREJA VULGARIS (L.) Fritsch [= *Clinopodium vulgare* L.] (LAMIACEAE).—Flat-head Co., Glacier National Park, along Going-to-the-Sun Road 10 km ne. of West Glacier, locally common in gravelly soil of road shoulder, 960 m, 15 Jul 1987, *P. Lesica and R. Potter 4400* (MONTU, NY) (verified by A. Cronquist, NY).

Significance. First report of this Eurasian species for MT and the Pacific Northwest.

SCLERANTHUS ANNUUS L. (CARYOPHYLLACEAE).—Missoula Co., road to Montana Power Station at the Rattlesnake Creek Dam ca. 2 km n. of Missoula, T13N R19W S2 ne.¼, large colonies along the fence in a horse corral, 1080 m, 20 May 1986, *K. H. Lackschewitz 10835* (MONTU, NY); along the n. bank of the Clark Fork River ca. 8 km nw. of Missoula, T13N R20W S1, common in sandy soil among river cobbles, 945 m, 27 Jul 1986, *P. Lesica and A. Bradley 3994* (MONTU, NY); Sanders Co., Beaver Gulch Road 5 km w. of Heron, T26N R34W S5 e.½, in drying vernal pools, 680 m, 4 Jun 1987, *K. H. Lackschewitz 11238* (ID, MONTU); Hutchins' house at the s. edge of Heron, T27N R34W S34, locally common in driveway gravel, 670 m, 15 Jul 1987, *P. Lesica 4399* (MONTU) (*Lackschewitz 10835* and *Lesica and Bradley 3994* verified by A. Cronquist, NY; *Lackschewitz 11238* verified by D. Henderson, ID).

Significance. First records of this Eurasian species for MT.

SPIRAEA × PYRAMIDATA E. Greene (ROSACEAE).—Lincoln Co., along Pete Creek 3 km w. of Yaak, T35N R32W S4, 915 m, 21 Jul 1965, *Mooar 753* (MONTU); Missoula Co., along East Fork Lolo Creek ca. 40 km sw. of Missoula, T11N R23W S28, marshy and mossy area, 1295 m, 19 Jul 1970, *Mooar 12743* (MONTU); Sanders Co., Bull

River Forest Service Campground 7 km nw. of Noxon, T26N R33W S10 n.½, under forest canopy, 700 m, 24 Jun 1986, *K. H. Lackschewitz 10909* (MONTU, NY) (verified by A. Cronquist, NY).

Significance. First records for MT. At all sites, this species occurs with *S. betulifolia* and *S. douglasii*.

STELLARIA GRAMINEA L. (CARYOPHYLLACEAE).—Sanders Co., Beaver Gulch Road 4 km w. of Heron, T26N R34W S4, common in grassy places along the road, 680 m, 4 Jun 1987, *K. H. Lackschewitz 11243* (ID, MONTU, NY) (verified by A. Cronquist, NY and D. Henderson, ID).

Significance. First report of this Eurasian species for MT.

THALICTRUM ALPINUM L. (RANUNCULACEAE).—Beaverhead Co., w. edge of Monida, T15S R6W S3, common on hummocks in a moist alkaline meadow, 2070 m, 27 Jun 1986, *P. Lesica 3918* (MONTU, NY) (verified by A. Cronquist, NY).

Significance. Although reported for MT by Hitchcock and Cronquist (Flora of the Pacific Northwest, 1973), this is the first confirmed record, a range extension of ca. 110 km w. from nw. WY.

VALERIANELLA LOCUSTA (L.) Betsche (VALERIANACEAE).—Lincoln Co., Slee Lake 3.2 km ne. of Troy, T31N R33W S6, formerly disturbed ground in a moist, acidic meadow, 770 m, 2 Jun 1987, *K. H. Lackschewitz 11226* (ID, MONTU, NY) (verified by A. Cronquist, NY and D. Henderson, ID).

Significance.—First report of this Eurasian species for MT.

WALDSTEINIA IDAHOENSIS Piper (ROSACEAE).—Missoula Co., e. of Fish Creek Road ca. 100 m past the crossing of Granite Creek ca. 40 km sw. of Missoula, T11N R23W S7 nw.¼, large colonies in open ponderosa pine forest, 1280 m, 9 Jun 1987, *K. H. Lackschewitz 11246* (ID, MONTU, NY) (verified by A. Cronquist, NY and D. Henderson, ID).

Significance. First report for MT. Previously known only from central ID, a range extension of 29 km e. from Idaho Co.—KLAUS LACKSCHEWITZ and PETER LESICA, Dept. Botany, University of Montana, Missoula 59812 and J. STEPHEN SHELLEY, Montana Natural Heritage Program, State Library Bldg., 1515 E. 6th Ave., Helena 59620. We are grateful to Ronald Hartman for providing records from the Rocky Mountain Herbarium.

WASHINGTON

ERIOGONUM DOUGLASII Benth var. *DOUGLASII* (POLYGONACEAE).—Ferry Co., Kettle Range, Colville National Forest, 2 km w. of Thirteen Mile Mt., T35N R33E S27, 1220 m, 25 May 1986, *Peterson and Annable 4230* (WS); 0.5 km s. of Thirteen Mile Mt., T35N R33E S33 s.½, 1070 m, 26 May 1986, *Peterson and Annable 4267* (WS). At both sites, common to dominant on shallow, loamy soils derived from andesite bedrock, associated with *Poa secunda* Presl and *Selaginella wallacei* Hieron.

Significance. First record for Ferry Co., a range extension of ca. 140 km n. from a previously reported site near Badger Mt., Douglas Co.—PAUL M. PETERSON and CAROL R. ANNABLE, Dept. of Botany and Ownbey Herbarium, Washington State Univ., Pullman 99164.

FESTUCA CALIFORNICA Vasey (POACEAE).—Ferry Co., Kettle Range, Colville National Forest, open grassy slopes with *Festuca idahoensis* Elmer, *Calamagrostis rubescens* Buckl., and *Pseudotsuga menziesii* (Mirbel) Franco., e. slopes of Mt. Leona, T38N R34E S25 n.½, 1800 m, 3 Jul 1985, *Peterson and Annable 3629* (WS).

Significance. First record for Ferry Co., previously known only from w. of the

Cascades in Skagit Co., a range extension of ca. 300 km e. of known locations on Fidalgo and Hat Islands.

LISTERA BOREALIS Morong. (ORCHIDACEAE).—Ferry Co., Kettle Range, Colville National Forest, needle duff below closed forest of *Picea engelmannii* Parry and *Abies lasiocarpa* (Hook.) Nutt., 1 km n. of Jungle Hill along Kettle Crest Trail, T36N R34E S1 sw.¼, 1830 m, 6 Jul 1985, *Peterson and Annable 3784* (WS).

Significance. First record for Ferry Co., a sensitive plant in WA previously known only from Okanogan Co., a range extension of ca. 50 km e. of the previously reported site near Mt. Bonaparte.

PHACELIA FRANKLINII (R.Br.) Gray (HYDROPHYLLACEAE).—Ferry Co., Kettle Range, Colville National Forest, 1 km nw. of Lambert Mt., T37N R34E S2 n.½, 1890 m, 3 Jul 1985, *Peterson and Annable 3651, 3652* (WS); trail junction between Midnight Mt. and Copper Butte, T37N R34E S11 se.¼, 1860 m, 19 Jul 1986, *Peterson and Annable 4482* (WS); e. of Copper Butte, T37N R34E S13 e.½, 1645 m, 19 Jul 1986, *Peterson and Annable 4502* (WS). Small populations were found on grassy slopes, along trails, and road berms beneath open forests of *Picea engelmannii* Parry, *Pseudotsuga menziesii* (Mirbel) Franco., and occasionally *Pinus contorta* Dougl.

Significance. First record for Ferry Co., a sensitive plant in WA previously known only from Okanogan Co., a range extension of ca. 45 km e. of the previously known reported site near Cayuse Mt.

ANNOUNCEMENT

WHITEBARK PINE SYMPOSIUM

A symposium entitled "Whitebark Pine Ecosystems: Ecology and Management of a High Mountain Resource" will be held 29–31 March 1989 at Montana State University. This symposium will explore the ecology and management of whitebark pine forests and associated resources of the high mountains in western North America—a subject of rapidly emerging recognition and importance. The symposium will conclude with a field trip into whitebark pine forests near Yellowstone National Park. The subject matter is intended for natural resource managers, research scientists, educators, specialists in wildlife, hydrology, soils, fire, recreation, range, silviculture, and others interested in high mountain resources. The symposium is co-sponsored by the U.S. Forest Service, U.S. National Park Service, Montana State University, and the Society of American Foresters who have designated it as a Regional Technical Conference.

For registration information or to be added to the mailing list, write to: University Scheduling and Conference Center, Room 280 F, Strand Union Building, Montana State University, Bozeman 59717, or call (406) 994-3333.

ANNOUNCEMENTS

NEW PUBLICATIONS

ALLEN, B. H., Ecological type classification for California: The Forest Service approach, *U.S.D.A. Pacific Southwest Forest and Range Experiment Station, General Technical Report PSW-98*, pp. [i], 1-8, Nov 1987, no ISSN, gratis (from Pacific Southwest Forest and Range Experiment Station, P.O. Box 245, Berkeley, California 94701).

CONRAD, C. E., Common shrubs of chaparral and associated ecosystems of southern California, *U.S.D.A. Pacific Southwest Forest and Range Experiment Station, General Technical Report PSW-99*, pp. [i], 1-86, July 1987, no ISSN, gratis (for address see entry for Allen). [Descriptions of and keys to 132 taxa; detailed glossary; appendix covers all genera including chaparral shrub and subshrub species recognized in P. A. Munz's *A flora of southern California* (1974).]

CONSTANCE, L., *Versatile Berkeley botanists: Plant taxonomy and university governance*, Regional Oral History Office, Bancroft Library, University of California, Berkeley, California 94720, 1988, 362-page interview, \$67.00 (or available for examination at Bancroft Library, UC Berkeley, or Dept. of Special Collections, UCLA). [An account of the "unending synthesis" of more than 50 years as a former UC Berkeley graduate student, professor, chair of the department, director of UC (the herbarium), dean of the College of Letters and Sciences, and umbellologist.]

CULLMANN, W., E. GÖTZ, and G. GRÖNER, *The encyclopedia of cacti*, trans. by K. M. Thomas, Alphabooks, Sherborne, Dorset DT9 3LN, 1986, 340 pp., illus. (most color), ISBN 0-906670-37-3 (hardbound), price unknown. [Translation of *Kakteen*, 2. Aufl., Eugen Ulmer GmbH & Co., 1984. A revision of a 1963 book by Cullmann by Gröner (esp. on cultivation and photos) and Götz (systematics). Sections on: structure, mode of living and classification of cacti; cactus culture; propagation of cacti; building up and accommodating a cactus collection; special cultural problems; genera and species of cacti (with keys); idem alphabetically arranged. Superb photos, with useful keys to taxa and clear descriptions.]

FULLER, T. C. and E. MCCLINTOCK, *Poisonous plants of California*, University of California Press, 2120 Berkeley Way, Berkeley, California 94720, 1986, [ii], vii, 433 pp., 16 pls. (color), illus. (B&W), ISBN 0-520-05568-3 (hardbound), \$25.00, ISBN 0-520-05569-1 (paperbound), price unknown. [= *California Natural History Guides*, no. 53. Contents: detailed descriptions of various taxa (294 pp.); plant toxins and derivative drugs (63 pp.); appendices (plants causing dermatitis, plants causing hay fever and asthma, plants accumulating nitrates); biblio.; indices. An immensely useful book, obviously not just for Californians—chock-full of fascinating information, e.g., tea mistakenly made of *Digitalis purpurea* instead of *Symphytum × uplandicum* leaves killed an elderly Washington couple in 1977. For review see D. Cheatham, *Fremontia* 16(1):30-31.]

COMMENTARY

MESSAGE FROM THE PAST CBS PRESIDENT

It is an honor and a pleasure for me to address the members of the society in this third report from the past President since the inception of the practice in 1986. It was particularly gratifying to note the response to a comment in last year's report in which Frank Almada expressed concern at the lack of graduate student response to financial support offered by the society to assist with their research. Several inquiries were received. It is nice to know that the membership reads these messages and responds to them.

As seems to be the case each year, the Society, through its Executive Council, faced a number of challenges in the last year. Not the least of these came with the realization that the costs associated with producing and distributing *Madroño* were once again taxing our resources. The Financial Officer estimated that costs associated with the journal would exceed the total income of the Society for the year. Clearly we could not continue on that basis. In an attempt to bring these costs under control and restore the Society to a sound financial status, the Council voted to reduce the number of free pages allotted to members to five (5) per volume. We realized that this would make it difficult for some authors but hope that members will be able use grant funds as well as funds from other sources to continue to publish in the journal. I should point out that for papers having joint authorship, the five page allotment applies for each author who is a member of the society.

One further step taken by the Executive Council this year was to reduce the maximum number of years of eligibility for student membership to five years. This is in line with the student membership period of other organizations and will help reduce the Society's deficit in producing *Madroño*.

By the time you read this the CBS Graduate Student Meetings will have concluded at San Jose State University. These meetings are sponsored by the Society and reinforce our commitment to the research of our graduate student members, recognize their outstanding work, and encourage communication between participating institutions. It is a time-consuming undertaking on the part of the graduate student representative and the Society owes a debt of gratitude to Valerie Haley of San Jose State for her efforts in organizing this year's meeting. These meetings take place at eighteen-month intervals. I encourage members to consider having their institutions host future meetings and, perhaps more important, I urge you to keep the meetings in mind and encourage your graduate students to participate. Papers are presented in categories of Proposed Research, Research in Progress, and Completed Research.

At the November 1987 meeting of the Council, proposals from graduate students for the Society's annual Graduate Student Research Award were reviewed. After consideration of the excellent proposals that had been submitted it was decided to make the award to Samuel Hammer of San Francisco State University for his project entitled *A Taxonomic Survey of the Lichen Genus Cladonia in California*. Mr. Hammer is a student of Dr. Harry Thiers. A check for \$250 was forwarded to Mr. Hammer to help support his investigation. I know that the membership of the Society joins me in offering our congratulations to Mr. Hammer. The procedures for applying for the Graduate Student Research Award are quite simple and I encourage all of the Society's graduate student members to consider submitting proposals to the Council. Requests for information and proposals should be sent to the current President of the Society. Proposals should reach the Society by 1 October each year. Now is the time to be thinking about a proposal for next year.

One final item, our annual banquet in February had the largest turnout in recent memory, thanks in no small measure to the speaker, Dr. Stephen J. Gould. It was a gala evening and enjoyed by all those in attendance. Our thanks to Dr. Peggy Fiedler, First Vice President of the Society for arranging an exciting program. By contrast the interesting monthly programs that Peggy arranged were attended by relatively few

members. This continues a trend of poor attendance that has been noted in recent years. I hope that members in the Bay Area will check the schedule of speakers for the coming year and plan to attend one or more of the regular meetings. It is hard to justify continuing monthly meetings with the present attendance.

It has been an honor for me to serve as President of the California Botanical Society for the past year and I thank you all for your support and advice. I must say, however, that the office of President is not what makes our society work. With the exception of the occasional "fire" the President has to put out, it is the volunteer members of the Executive Council that do all of the day-to-day chores that make things run smoothly. The names of those people are listed inside the front cover. I think that the membership of the Society owes those individuals a debt of gratitude for their hard work, and I know that I do. Thanks to all of you.—DALE W. MCNEAL, Department of Biological Sciences, University of the Pacific, Stockton, CA 95211.

ANNOUNCEMENT

NEW PUBLICATIONS

MICKEL, J. T., with contributions by R. McVAUGH, S. KARELL, and H. BALSLEV, Liebmann's Mexican ferns: His itinerary, a translation of his "México's Bregner," and a reprinting of the original work, *Contributions from the New York Botanical Garden*, vol. 19, pp. [i-v], 1-173-[175-350], 27 Oct 1987, ISSN 0736-0509, ISBN 0-89327-324-4, \$30.50 U.S., \$31.75 foreign, postpaid (for address see entry for Austin et al.). [On Frederik Michael Liebmann's (1813-1856) rare 1849 work describing 308 spp., 95 new. Contents: introduction (Mickel); itinerary and gazetteer (McVaugh); the translation (Karell and Balslev); index to the translation; the reprint on pp. 175-end.]

MOZINGO, H., *Shrubs of the Great Basin: A natural history*, University of Nevada Press, Reno, Nevada, 1987, xvii, [ii], 342 pp., 24 pls. (color), illus. (B&W), ISBN 0-87417-111-3 (hardbound), ISBN 0-87417-112-1 (paperbound), prices unknown. [Lengthy, somewhat rambling, occasionally botanically inaccurate (e.g., *Ephedra* "flowers"), but still interesting and quite useful descriptions of 66 spp. in 25 fam.]

WARREN, B., *Wilderness walkers: Naturalists in early Texas*, Hendrick-Long Publishing Co., P.O. Box 25123, Dallas, Texas 75225, 1987, 112 pp., illus., ISBN 0-937460-26-5 (hardbound), \$12.95. [Excellent children's books on seven "walkers," horseback riders, coachmates, and just wanderers across Texas: Berlandier, Drummond, Lindheimer, Wright, Audubon, Roemer, and Lincecum.]

EDITOR'S REPORT FOR VOLUME 35

This annual report provides an opportunity for the editor to communicate the status of manuscripts received for publication in *Madroño* and to comment on the other aspects of the journal. Between 1 July 1987 and 30 June 1988, 52 manuscripts were received (29 articles, 6 notes, and 17 noteworthy collections contributions totalling 57 individual taxa). Since 30 June 1988, 26 manuscripts have been received (14, 7, 5). The current status of the 51 unpublished manuscripts is 8 in review (7, 1, 0), 20 in revision (16, 4, 0), 8 needing decision by the editor (6, 2, 0), and 15 accepted for publication (8, 3, 4). There are 4 unpublished book reviews. Volume 35 included 62 published manuscripts (31, 6, 16), 5 book reviews, and 2 commentaries or letters. The period between submittal and publication averaged 14 months for articles. Five manuscripts were rejected, and 3 were withdrawn by the author. At the beginning of my editorship I inherited several manuscripts that had been returned to authors more than one year previously; the authors of 11 of these did not respond to my inquiries about the status of the manuscripts, and I consider these manuscripts to have been withdrawn.

Several individuals have been of much help to me as I took on the responsibilities of Editor. Wayne Ferren, the outgoing Editor presented me with a healthy journal with manuscripts in various stages of processing. Wayne gave me the opportunity to gradually assume the editorial reins during a transition period in the fall of 1987. Wayne's help was invaluable in getting my term as Editor off to a smooth start. He has continued to be an excellent source of advice when I have felt the need for counsel on journal matters. In addition he made arrangements to provide the excellent photograph of C. H. Muller to whom this volume is dedicated and arranged to have Dale Smith write the dedication. Steven Timbrook has continued to serve the Society both as a member of the Editorial Board and by preparing the annual Index and Table of Contents.

My thanks also go to the authors whose papers I have edited for their patience and tolerance as I have learned the job of Editor. I have, on occasion, taken longer than authors would have liked to process the manuscripts. Sometimes the fault is mine; sometimes it is out of my hands. I thank authors for their frank comments when I have made mistakes.

With volume 35 *Madroño* began the publication of Spanish language manuscripts and abstracts. To date we have published only one article in Spanish. An additional 10 articles in English that pertain to Latin American topics have Spanish abstracts. Raul Cano, a colleague here at Cal Poly, has been of much assistance to me and to several authors in the preparation of Spanish abstracts. On behalf of the Editorial Board I encourage Latin American members of the California Botanical Society to submit Spanish-language manuscripts to *Madroño*.

Articles and notes in *Madroño* reflect the wide-ranging interests of the members of the California Botanical Society. Topics discussed in volume 35 include cytology, ecology, floristics, hybridization, nomenclature, paleobotany, phytogeography, and systematics. The papers represent research in widely dispersed geographical areas including Canada, various parts of the United States, Mexico, Nicaragua, Ecuador, and Peru. *Madroño* continues to serve as a source of additional information as well through reviews and announcements that inform members of the Society of publications, meetings, and other topics of interest. As Editor, I encourage potential authors to continue to submit manuscripts that maintain the broad cross-section of botanical topics.—D.J.K. 5 Dec 1988.

REVIEWERS OF MANUSCRIPTS

As Editor, I thank all reviewers for their assistance with manuscripts. Special thanks are extended to those who reviewed several manuscripts published in 1988. I am very grateful to each reviewer for his or her generous contribution of time and effort. The quality of papers published in *Madroño* reflects this contribution. Reviewers for volume 35 are:

George W. Argus
Daniel I. Axelrod
Mary E. Barkworth
Rupert C. Barneby
Mark Borchert
Mary C. Carroll
Annetta Carter
Kenton L. Chambers
Curtis Clark
Martin L. Cody
Susan Conard
Lincoln Constance
William B. Critchfield
Arthur Cronquist
Thomas Daniel
Carla D'Antonio
Frank W. Davis
D. Douglas
Patrick E. Elvander
Barbara Ertter

Amy Jean Gilmartin
Lisa Graumlich
James R. Griffin
James W. Grimes
William L. Halvorson
Emily L. Hartman
Ronald L. Hartman
James Henrickson
Duane Isley
David Keil
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Malcolm G. McLeod
Dale McNeal
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Kevin Nixon
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Donald J. Pinkava

Rhonda Riggins
Reed C. Rollins
Jerzy Rzedowski
John O. Sawyer
Mark A. Schlessman
Theresa Scholars
James Shevock
Paul C. Silva
James P. Smith
John Stechman
John Strother
Barry Tanowitz
Dale Thornburgh
Steven Timbrook
Thomas Van Devender
Frank Vasek
Nancy Vivrette
William A. Weber
Dieter H. Wilken

ANNOUNCEMENT

NEW PUBLICATION

HEWSON, H. J., *Plant indumentum: A handbook of terminology*, *Australian Flora and Fauna Series*, no. 9, pp. i-vii, 1-27, 1988, ISSN 0813-6726, ISBN 0-644-50456-0, Aust \$4.95 (from Australian Government Publishing Service, Box 84, Canberra, A.C.T. 2601). [Intended esp. for writers of the *Flora of Australia* to standardize terminology. Contents: intro; basic concepts; description formula; glossary and key to terms; biblio.; index. Each term is clearly described and figured, usually with diminutive and adjectival forms of the term, derivation of the term, examples. "The use of plain English descriptive terminology is encouraged, e.g., 'bifid T-shaped trichome' is preferred to 'Malpighiaceus' (p. 1).]

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